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THE STRENGTHENING SYSTEM IN THE STEM OF MAIZE*

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ABSTRACT

The system providing strength to a maize stem is described as consisting of thick-walled, lignified cells located in three distinct stem tissues: hypodermis; peripheral bundle sheaths; and sclerified ground parenchyma. Striking changes occur in the disposition of these tissues from the base of a stem to the apex, which are directly related to the plant's mode of development. Inter-racial differences in amount and arrangement of sclerotic tissue are described, and contrasted with the strengthening systems of *Euchlaena* and *Tripsacum*. WILLIAM H. MURDY, Emory University, Atlanta 22, Georgia.

INTRODUCTION

The species *Zea mays* is characterized today by an almost overwhelming range of variability; a consequence attributed in part to its unique history in association with ethnic groups of man in the New World, and in part, to former introgression with the genus *Tripsacum* and the present ability to exchange germ plasm with *Euchlaena* (teosinte; a genus of putative hybrid origin between *Zea* and *Tripsacum*).

The concept of race has been advanced as a step toward a natural classification of this variability. Anderson and Cutler (1942), largely responsible for the evolution of this concept, defined a race loosely as a "population of maize plants differing from other groups by a great number of genes and sharing enough characters in common to be easily recognized as a distinct group".

For the past several years, the Rockefeller Foundation in collaboration with Latin American countries has been performing the arduous task of classifying indigenous races of maize in Central and South America. The character of scleroticness, as expressed by features such as stalk stiffness, the coarseness of leaves and cob induration, is one of many polygenic characters by which races of maize have been found to differ. The magnitude of tissue induration is frequently accepted as evidence of teosinte or *Tripsacum* contamination, since highly sclerotic plants often exhibit other plant characters regarded as "tripsacoid" in nature (Wellhausen, 1952). Moreover, segregates from maize-teosinte crosses often

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possess an inordinate degree of tissue induration (Mangelsdorf and Cameron, 1942). Galinat et al. (1956) state that "extensive experiments with maize-teosinte hybrids have demonstrated that genes responsible for lignification occur on many, if not all, of the chromosomes of teosinte".

The character of sclerification, when properly evaluated, should add materially to our knowledge concerning the origin of modern maize and its past and present relationship with *Euchlaena* and *Tripsacum*. The present study was undertaken in order to shed light on the following basic questions: (1) What stem tissues become sclerified to make up the strengthening system and how do these tissues differ in amount and arrangement from the base of a stem to its apex? (2) What is the range of variability within and between races of maize in respect to the strengthening system? (3) What relationship exists between the strengthening system of maize and that of *Euchlaena* and *Tripsacum*?

One of the foremost requisites of good breeding stock is an ability to stand up well and contribute a fair share of stalk-stiffness in crosses. Several anatomical studies, based on the lower internodes of inbred lines, have established a correlation between lodging resistance and the nature of sclerotic tissue (Magee, 1948; Hunter and Dalbey, 1937). The results of these investigations are valuable to the corn breeder, but have only an indirect bearing on the nature of sclerotic, strengthening systems in vigorous open-pollinated races.

MATERIALS AND METHODS

Six maize races were selected from the "Standard Exotics" described by Anderson and Brown (1951), which represent the extremes of variation in *Zea mays* growable in the corn belt. Many plants of each race were grown under essentially uniform field conditions at the Pioneer Hi-Bred Corn Company, Des Moines, Iowa. Following is a brief description of each race.

Gourdseed (Brown and Anderson, 1948)—An old southern dent variety typical of the kind of maize commonly grown in southeastern United States in colonial times. This particular stock was collected by Dr. W. L. Brown in 1946 at Grapevine, Texas. Plants are generally tall, having many internodes, few tillers, and greatly condensed ears and tassels. Chromosome knob numbers medium high (5-7); plants mature slowly (approximately 94 days from planting to silk in Iowa).

Northern flint (Brown and Anderson, 1947)—Representative of the maize once grown almost exclusively in the northern and eastern sectors of the United States until superseded by early corn-belt varieties. Plants vary somewhat throughout their range, but share many features in common including low chromosome knob numbers (0-2), eight-rowed ears, few, but long internodes (those above the ear not decreasing in length as in the case of Gourdseed), several tillers shorter in height than the main stem, and a rapid growth rate (from planting to silk in Iowa takes approximately 66 days).

Argentine pop (Anderson and Brown, 1951)—A small-eared, prolific pop corn race of Paraguay and Argentina. Unlike the other five races, Argentine pop has not likely been contaminated by either North American *Tripsacum* or teosinte. Furthermore, its ear is closest to the concept of prehistoric South American maize

based on archeological evidence. It grows slowly in Iowa and at maturity consists of a main shoot with many short internodes relatively equal in length, plus a few tillers shorter than the main culm. Planting to silk requires approximately 105 days.

Chapalote (Wellhausen, 1952)—A pop corn race grown in the coastal lowlands of northwestern Mexico. Plants are "tripsacoid" in appearance in the possession of several long, ear-bearing tillers approaching in height the main shoot, long internodes, and long narrow leaves. Wellhausen classified this race as a primitive, indigenous pop corn with little evidence of teosinte contamination. Chromosome knob number is variable; the average is approximately six. About 90 days are required from planting to silk in Iowa.

Papago (Anderson and Cutler, 1942)—Seed of this race was obtained from the Papago Indians in the desert south of Tucson, Arizona. It is typical of the maize grown by desert-dwelling Indians and similar to archeological maize grown by the prehistoric Basketmakers—the first agriculturalists of this region to leave a record (Anderson and Blanchard, 1942). Its habit resembles that of Chapalote; long ear-bearing tillers, long internodes, and long narrow leaves. Chromosome knob number is medium high and growth rate quite rapid (approximately 77 days from planting to silk in Iowa).

Zapalote chico (Wellhausen, 1952)—An extremely sclerotic race grown in the coastal lowlands of southern Mexico. Plants are coarse and indurate, lack tillers, and have many short internodes above the ear. Chromosome knob number is high (12–16) and Wellhausen considers this race to be highly contaminated with teosinte germ plasm. It matures rapidly in its native habitat and is comparatively independent of day length when grown in Iowa. Planting to silk requires approximately 81 days.

Six plants of Florida teosinte (*Euchlaena mexicana*), from a commercial source, were used in this study; two were grown in Iowa and four in Florida. Plants from two separate clones of *Tripsacum dactyloides* were sampled; one growing in Iowa and the other located in St. Louis, Missouri. A single plant of *Tripsacum lanceolatum* collected in Guatemala by Dr. E. Anderson was also included in this study.

Just after anthesis, 15 plants of each maize race were selected in an attempt to adequately sample the range of morphological variability within races. Plants were collected when completely mature and subsequently subjected to morphological and anatomical analysis. In making anatomical sections of desiccated stems, internodal discs about 2 cm. long were boiled in water, with aerosol added, for approximately 4–5 hours; placed in 50 percent alcohol overnight; sectioned with a sharp razor; stained with safranin and fast green; and permanently mounted in piccolyte, a synthetic mounting medium.

MATURATION OF A MAIZE STEM

The stem of maize can be looked upon as a series of alternating segments, or phytomers (Evans and Grover, 1940). Each phytomer is made up of an internode, with a leaf at its upper end and a bud at its base. Final maturation of a phytomer begins in the leaf blade, passes down the leaf sheath and finally down the internode

below. Successive phytomers, however, mature acropetally up to, but not including, the tassel peduncle, which together with its tassel does not await the ascending wave of maturation, but matures relatively early at a time when the internodes immediately below are still immature. Normally there is no leaf associated with the tassel peduncle, thus, internodal tissue maturation begins in the upper portion of this internode. By measuring internode lengths of genotypically uniform hybrid plants at various stages of maturity, one is able to obtain a picture of the ontogenetic pattern of stem development (fig. 1). Note the plant examined ten weeks after planting; it is still relatively immature, nevertheless, the leafless peduncle is already 11 cm. long, almost half its assumed maximum length, while the two internodes immediately below, associated with leaves, are merely 2 cm. in length, only one-ninth their assumed maximum length at maturity.

A similar pattern of maturation was reported by Prat (1935) for stems of *Secale cereale*. He noted that the terminal internodes bearing the inflorescence elongated more rapidly than the subterminal internode. By subjecting these two internodes to mechanical stress, he found the uppermost to be more resistant. He concluded that rapid maturation accompanied rapid elongation and that both processes occurred faster in the terminal internode than in the one below.

It is likely that the maturation of a maize stem conforms to a pattern widespread in the Graminae. Knowledge of this pattern is essential to an understanding of maize stem anatomy, for the rate at which an internode grows and matures has a direct bearing on its internal structural features.

STRENGTHENING TISSUES IN A MAIZE STEM

In herbaceous monocots generally, mechanical stem strength is provided by thick-walled sclerotic tissue. The process of cell sclerification entails the deposition of a thick, cellulosic secondary wall and subsequent impregnation of primary and secondary walls with lignin. Tissues that contribute most to the strength of a maize stem can be classified in three categories: (1) sclerenchyma associated with vascular bundles; (2) hypodermal sclerenchyma; (3) sclerified parenchyma.

Vascular bundle sclerenchyma. A maize stem in cross-sectional view (plate VI, D) shows a scattered arrangement of vascular bundles surrounded by parenchymatous ground tissue. Those bundles near the periphery of the stem are crowded, small and generally provided with heavy sclerotic sheaths, whereas the more central ones are widely-spaced, larger in size, and lack massive sheaths. The presence of two distinct vascular systems in maize has previously been reported. Both Esau (1943) and Cutler and Cutler (1948) reported two systems in the stem. The latter authors referred to the outer system as the "peripheral" and the inner as the "central". Two quite dissimilar systems have also been noted in the ear (Lenz, 1948; Laubengayer, 1949; Reeves, 1950) and tassel (Kumazawa, 1940).

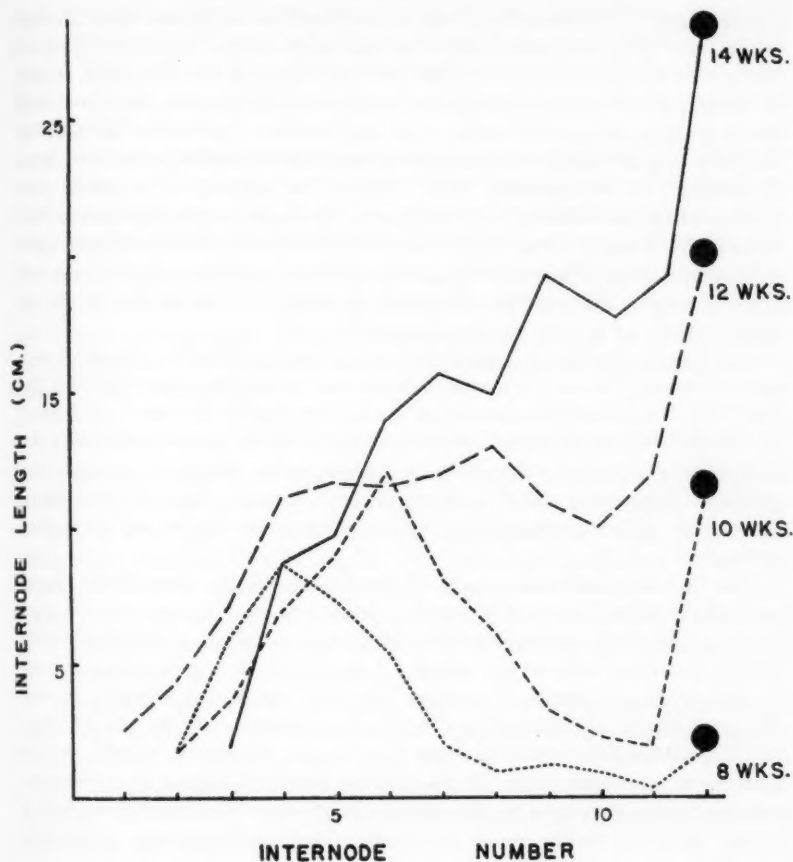


Fig. 1. Internode diagrams of genotypically identical plants measured at intervals of 8, 10, 12, and 14 weeks after planting. Successive stem internodes elongate acropetally except for the tassel peduncle.

The leaves of maize are vascularized by large, early-maturing bundles and smaller late-forming bundles which alternate with the larger ones. At a node, the large leaf bundles pass some distance into the stem at a right angle before assuming a vertical or oblique course down through the internode below. Ontogenetically, the large bundles originate at the node and simultaneously differentiate in two directions; up into the leaf and down through the internode before either of these organs have completed their elongation. Only when acropetal differentiation of these large bundles reaches the tip of the leaf blade, do the small alternating

bundles begin to differentiate basipetally in the distal part of the leaf blade, developing at a time when most elongation of leaf and stem has been completed (Sharman, 1942). At a node these small bundles pass into a ring of vascular tissue, formed by the lateral anastomosis of peripheral strands from the internode above, and their sheaths become merged with those of the ring bundles. Just below the node the peripheral ring of vascular tissue breaks up into distinct bundles, which pass down the periphery of the internode below. Hence, the majority of peripheral stem bundles, which play a leading role in support of the stem, are prolongations of late-maturing leaf bundles. Some of the smallest bundles found in the peripheral region of the stem have an even later origin in the intercalary meristem region at the base of a leaf sheath. Esau (1943) illustrated the origin of such bundles within the massive sheaths of large, early-maturing bundles.

All vascular bundles of appreciable size are associated with a sheath of protective fiber cells, heaviest at the protophloem and protoxylem poles (plate VI, B). Esau (1943) described the ontogeny of the vascular bundle in maize. She pointed out that the fibers of the sheath originate mainly from the procambium which also gives rise to the vascular tissue itself; in addition, tissue adjacent to a bundle may contribute cells to the sheath in its somewhat advanced stage of development. The amount of such accretion varies with the size of the bundle and its location in the plant.

The vascular bundles with associated sheath sclerenchyma comprise the "backbone" of the skeletal structure supporting the stem of a maize plant. In the form of strengthening rods passing discretely through parenchymatous ground tissue the bundles contribute little to the support of the plant. It is only when they are arranged in various structural patterns that their mechanical function is most effective. The peripheral bundles with prominent sheaths, may, by the sclerification of inter-bundle parenchyma, form a continuous supporting cylinder, at least in the lower internodes (plate VI, A). Similar peripheral bundles in upper internodes are frequently welded to the epidermis by a bridge of sclerotic tissue derived in part from the bundle sheath and partly from the hypodermis (plate VII; D, E, F).

Hypodermis. Immediately beneath the epidermis of a maize stem is a zone of thick-walled, elongate fiber cells (plate VI, A). This tissue, commonly known as a hypodermis, is lacking or poorly developed in lateral and foliar organs. Frequently the hypodermis is very thick in its radial dimension and makes a substantial contribution to the strength of certain parts of the stem.

Ontogenetically, the subepidermal meristematic cylinder which gives rise to the hypodermis probably originates from the "flank meristem" of Ledin (1954). Popham (1951) refers to this histogen as a peripheral meristem forming a cylinder between the protoderm, which gives rise to the epidermis, and central meristem, which develops into pith and procambial strands. In ontogeny, parenchyma cells underlying the epidermis undergo longitudinal divisions and as the internode elongates, these initials do not undergo transverse division, but grow rapidly in the

axial direction resulting in the development of long narrow fibers (Hayward, 1938). Hypodermal fibers isolated from plants of the race Papago average 1.2 mm. in length and are $100\times$ longer than broad. During growth, the tips of the fibers push past one another resulting at maturity in a very strong non-storied peripheral cylinder.

Accentuated development of hypodermal sclerenchyma is found just above the point where a leaf or lateral branch departs from the main stem. This fact may have a significant bearing on the problem of intense sclerification of the cob rachis where the internode above each lateral branch (spikelet pair) is greatly abbreviated.

Sclerified parenchyma. Parenchymatous tissue in the outer region of a stem frequently becomes thick-walled and lignified to an extent that differs greatly among internodes of a single plant. When well-developed, the sclerotic parenchyma takes the form of a thick, subepidermal, sclerotic cylinder pervaded by peripheral vascular bundles (plate VII; A, B).

CHANGES IN THE STRENGTHENING SYSTEM OF AN INDIVIDUAL STEM

Structural changes in anatomy from one internode to another have not been described for maize, but are known in other grasses. Prat (1935) found internodes to vary in their ability to withstand mechanical pressures. The lower internodes were strongest in this respect with resistance diminishing acropetally. Athanassoff (1928) described the anatomy of successive internodes of a wheat culm. He found that internodes differed in the relative amount and arrangement of sclerenchyma, parenchyma, and vascular tissue. He also noted that internodes differed in respect to their time of maturation.

Anatomical sections of six internodes from the stem of a single plant are pictured in plate VII. The principal structural differences among internodes include the following: variation in size, shape, and sheath development of peripheral vascular bundles; differences in the relationship of these outer bundles with subepidermal sclerenchyma; and, changes in the extent of hypodermis and sclerified parenchyma development.

Peripheral vascular bundles. The peripheral bundles are very small in the lowermost internode (plate VII, A), but increase in size acropetally. In the internodes below the ear (plate VII; A, B, C) peripheral bundle sheaths, though massive, show very little centrifugal development, and between sclerenchyma at the proto-phloem end of the bundles and sclerenchyma of the hypodermis is a zone of thin- or thick-walled parenchyma. Peripheral bundles in the internodes above the ear (plate VII; D, E, F) are large in size and rhomboid in shape. These bundles have a much greater development of sheath sclerenchyma at the proto-phloem pole which, being confluent with the hypodermis, results in the formation of sclerotic "bridges" connecting the peripheral bundles to the epidermis.

The small, peripheral bundles in the lower internodes (plate VII; A, B) evidently matured after these internodes had ceased to elongate. They have little proto-phloem and protoxylem and are relatively unstretched, as evidenced by the

lack of a protoxylem lacuna (Esau, 1943). Their complete dissociation from the hypodermis and sub-epidermal parenchyma infers that their development in the internode occurs after these outer stem tissues have matured. In the internode just below the lowest ear (plate VII, C) peripheral bundles are somewhat larger than in lower internodes. In addition, they possess protoxylem and the middle bundle is somewhat stretched. Therefore, up to this point, there is an acropetal narrowing of the time lag between the maturation of the outer internodal tissues and the peripheral bundles. From the next internode on into the tassel the anatomy of the stem undergoes a striking change (plate VII, D). In these upper internodes, peripheral bundles differentiate prior to the completion of internode elongation and at a time when the outer tissues of the internode are still immature and capable of further division and elongation. As a result, these bundles are large, with well developed protoxylem and protophloem, and a large protoxylem lacuna. Moreover, bundle sheaths are well developed at the protophloem pole and confluent with hypodermal sclerenchyma. Except for size, the peripheral bundles in the peduncle and tassel (plate VII; E, F) are comparable to those of the internodes immediately below and are similarly bridged to the epidermis.

The structural variation of vascular bundles in the corn stem described above is attributable to differences in the relative period of development and maturation of outer stem tissues and the vascular bundles descending through them from leaves above. Starting with the lowermost internodes where the peripheral bundles develop some time after the completion of internode elongation, there is a gradual change in this relationship whereby the development and maturation of the two tissues is progressively more closely approximated. At a point where the lowermost ear is borne, the development and maturation of the two tissues is coincident. Sharman (1943) has pointed out that the time taken for the internode to complete its development increases with the maturity of the plant. He noted that "in the upper internodes there may be a lapse of four or more plastochrones between the full expansion of the lamina and internode." In other words the development and maturation of leaves with their included vascular strands, occurs at a fairly uniform rate acropetally, whereas the maturation of tissue in successively higher internodes progressively slows down.

An internode pattern of this plant (fig. 4, lower right) shows that the lower internodes (aside from the first two above the ground), which on the basis of anatomy were found to mature rapidly, are elongate, whereas the slower-maturing, upper internodes have relatively short lengths. Consequently, the changes in the length of internodes coincides with the changes in structural anatomy and both reflect the particular growth behavior characteristic of this plant.

Hypodermis. The greatest development of hypodermal sclerenchyma occurs in the middle internodes of the plant (plate VII; C, D), diminishing in extent below (plate VII; A, B) and above, where it is found only opposite bundles in peduncle and tassel internodes (plate VII; E, F). The lower internodes and tassel mature more rapidly than internodes between and those just beneath the peduncle are the slowest to mature. It is precisely in these short, upper internodes, having the slowest rate of maturation, that the hypodermis has its greatest development.

Sclerified parenchyma. In the upper internodes intervening parenchyma between peripheral bundles is firm, but relatively thin-walled and unligified. Intense sclerification of ground parenchyma occurs in internodes quite low on the plant (plate VII; A, B). The lower internodes are the earliest to originate and have a longer period of time to deposit cell wall material. In addition, there is a great basipetal flow of sugar through these lower internodes especially in the early stages of the plant's growth. The upper internodes have a longer period to differentiate fiber cells, but a shorter period for these cells to deposit cell wall material prior to final desiccation. Furthermore, after fertilization of the ear a great amount of sugar is channeled into the developing kernels causing a drain on the availability of sugars required for the synthesis of cellulose in late-developing internodes.

RACIAL VARIATION IN THE STRENGTHENING SYSTEM OF MAIZE

Hypodermis. In all races examined (except Argentine pop) hypodermal tissue develops to its greatest extent in the upper stem internodes between ear and tassel. It is suggested that prolonged activity of the peripheral meristem in these upper, slower-maturing internodes results in the differentiation of a great number of hypodermal fiber cells prior to tissue maturation. Races differ, however, in the extent of hypodermal tissue development, which may in part result from a dissimilarity in growth behavior. For example, plants of the race Gourdseed consistently have a thicker hypodermis (greater radial number of fiber cells) than do plants of the race Northern flint (plate VIII; B, D). As a race, however, Gourdseed is characterized by having a slow rate of growth and a series of short slow-maturing internodes above the ear shoot—the region of greatest hypodermal development in all races. Northern flint plants, on the other hand, have a rapid growth rate and the upper internodes are long and relatively quick to mature. Therefore, when comparing the potential ability of these two races to produce hypodermal sclerenchyma, their respective growth patterns must not be overlooked. Although in most races the upper internodes invariably mature more slowly than middle and lower ones, the race Argentine pop is characterized by a very uniform rate of growth resulting in all internodes being short and relatively slow to mature. In plants of this race middle internodes of the stem show the greatest extent of hypodermal development (plate IX, B).

Growth rate does not wholly account for the hypodermal differences observed among races. Papago, the race with the thickest hypodermis (plate VIII, A), is one of the most rapid to mature. In this race, however, the unusually heavy hypodermis is associated with deep-lying peripheral vascular bundles and both features may have definite selective value for such a semi-xerophytic race in diminishing the extent of water loss from stem tissues.

The amount of hypodermal tissue development in plants of a particular race is fairly uniform. Where intra-racial differences do occur, they are accompanied by changes in the overall scleroticness of the plant. When the width of the hypo-

dermal zone is measured in the internode of its greatest development, races of maize analyzed line up from greatest to least in the following manner: Papago (plate VIII, A); Gourdseed (plate VIII, B); Zapalote chico (plate VII, D); Chapalote (plate VIII, C); Argentine pop (plate IX, B); Northern flint (plate VIII, D).

Hypodermal tissue is not a prominent feature in the stems of teosinte plants examined (plate VIII, E). *Tripsacum* likewise lacks an appreciable development of continuous hypodermal tissue. The strengthening system of *Tripsacum*, however, is characterized by separate, peripheral strands of procambial tissue which at maturity form sclerotic connections between peripheral vascular bundles and epidermis. Thin-walled chlorenchymatous tissue lies between adjacent girders.

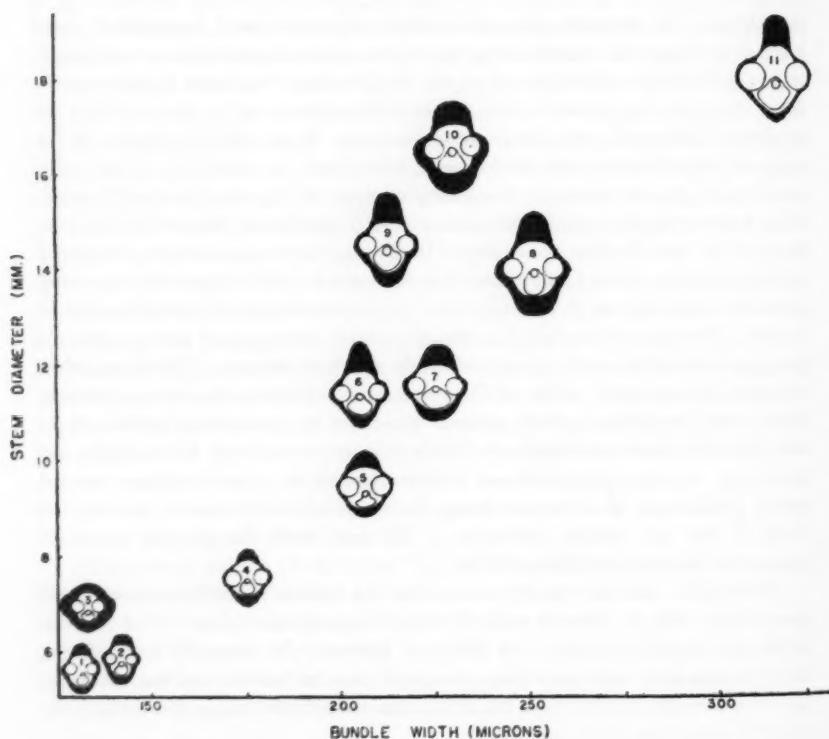


Fig. 2. Pictorialized scatter diagram to show the relationship of bundle width to stem diameter and amount of bundle sheath sclerenchyma for six races of maize plus teosinte and two species of *Tripsacum*. 1, *Tripsacum dactyloides*; 2, Teosinte grown in Florida; 3, *Tripsacum lenceolatum*; 4, Teosinte grown in Iowa; 5, Argentine pop; 6, Gourdseed; 7, Chapalote; 8, Northern flint; 9, Zapalote chico; 10, Papago; 11, Gourdseed (extreme plant).

Vascular bundles. The vascular bundles found in any cross section of a corn stem vary in size, shape, and also in their amount of associated sheath sclerenchyma (plate VI, D). Just inside the outer ring of heavily sclerotic bundles is a zone of strands, intermediate in character between the small, often reduced peripheral strands and the large, greatly stretched central ones. This ring of bundles is most easily discerned in the upper internodes of a corn stem and within a particular internodal cross section bundles are remarkably uniform in all their features. Determinations of bundle size were carried out on five such bundles (one appears on plate VI, B) from the fourth internode below the peduncle in each plant studied. Bundle size refers only to the dimensions of the vascular tissue within the bundle sheath.

Vascular bundle size varies somewhat among plants of a single race, but to a greater extent from plants of one race to those of another. Nevertheless, in both instances there exists a strong correlation between the diameter of a particular internode and the size of its contained bundles. The relationship of bundle size to stem diameter for five races of maize plus teosinte and two species of *Tripsacum* is diagrammed in fig. 2. Each symbol represents the average bundle dimensions of a race with the relative amount of sheath sclerenchyma in black. The races Papago (10), Northern flint (8), Zapalote chico (9), and most Gourdseed plants (6) show a heavy development of sheath sclerenchyma in proportion to bundle size, especially when compared with Chapalote (7), Argentine pop (5), and teosinte (4). Relative to bundle size, sheath sclerenchyma is weakly developed in teosinte, greatly developed in *Tripsacum dactyloides* (2), and massive in *Tripsacum lanceolatum* (3).

Peripheral stem bundles become progressively smaller and more reduced in successively lower internodes. This change is accompanied by an increase in their associated sheath sclerenchyma. Moreover, the walls of the fiber cells constituting the bundle sheath become thicker in successively lower internodes.

All plants of the race Zapalote chico conform to the structural pattern shown by the plant pictured in plate VII in that most of the peripheral bundles of upper internodes are connected to the epidermis by a sclerenchymatous bridge. A similar pattern, however, is not found in all races of maize. For bridging to occur in any plant internode it is necessary that the peripheral bundles lie close to the epidermis and that sufficient bundle sheath sclerenchyma develops at the phloem poles prior to the maturation of sub-epidermal tissue.

Papago has deep-lying peripheral bundles and though heavily sclerotic, none are bridged to the epidermis in any stem internode. Plants of the race Chapalote vary in their incidence of bridging, but the variation is correlative with peripheral bundle distance from the epidermis. On the other hand, proximity of peripheral bundles to the epidermis is not solely responsible for the incidence of bridging, either in a single stem or in a race. For example, peripheral bundles in all internodes of a teosinte stem lie close to the epidermis, but bridging only occurs in the peduncle and upper one or two internodes (plate X, A). In respect to races, all

peduncles of Zapalote chico plants studied have over fifty per cent of their peripheral bundles bridged to the epidermis, even when these bundles lie 150 microns from the epidermis (a distance greater than that of unbridged Chapalote plants). On the other hand, the peripheral bundles in the stems of Argentine pop lie relatively close to the epidermis, but are unbridged.

Considering only the phenomenon of bridging in maize, teosinte and *Tripsacum*, the following classification can be made.

1. *No bridging in any internode of the plant.* This condition is found in Argentine pop (plate IX; A, B) and in the North American pop corn race, Ladyfinger.
2. *Bridging in the tassel, tassel peduncle and 2-3 internodes below.* Northern flint, Zapalote chico (plate VII; A-F), Gourdseed (plate IX; C, D), Chapalote, and teosinte (plate X; A, B.)
3. *Bridging in all plant internodes.* *Tripsacum dactyloides* (plate X; C, D) and *Tripsacum lanceolatum*.

The lack of bridging in Argentine pop may be due to the distance of peripheral strands from the epidermis, paucity of sheath sclerenchyma, or both. It is possible, however, that it is in part a result of a particular pattern of growth, basically different from both *Tripsacum* and the races of maize which exhibit bridging. Argentine pop plants have a very slow growth rate and at maturity each plant consists of a great number of short internodes differing little in length (fig. 4). The longest internode occurs in the lower one-third of the plant. Beyond this point successive internodes gradually diminish in length up to the tassel peduncle, which itself is seldom longer than the internode next below and barely, if at all, exerted beyond the uppermost leaf sheath. Peripheral bundles are uniformly small and unstretched throughout the length of the plant. This infers that in each internode the peripheral bundles mature after the completion of tissue elongation. Hence, in all internodes of the stem, internodal tissue and peripheral bundles mature at a rather uniform rate, the former keeping ahead of the latter.

The presence of bridging in upper plant internodes but not in those below has been described for Zapalote chico (plate VII) and attributed to an extreme retardation in the rate of maturation of internodes above the ear shoots. A similar change occurs in the slow-maturing race Gourdseed, which like Zapalote chico, is characterized by a series of very short internodes between the ear and tassel.

Northern flint and teosinte grow rapidly and the upper internodes slow down only slightly in their rate of growth and maturation (fig. 4). As in Gourdseed and Zapalote chico, the peduncle and upper one or two internodes exhibit bridging. Such bridging is likely the result of a speeded-up maturation of peripheral bundles coupled with a slight decrease in stem tissue maturation, for the upper 2-3 leaves are always very much shorter than those below. Hence, the peripheral bundles have a much shorter distance to differentiate before reaching the stem. In the case of Zapalote chico, the change in peripheral bundle configuration is abrupt; in Northern flint and teosinte it is gradual. For example, in one plant of teosinte,

eighty percent of peripheral bundles in the peduncle were bridged to the epidermis, fifty percent in the internode below, fifteen percent in the next lowest internode and zero percent in the one below that.

In the genus *Tripsacum*, the formation of girder sclerenchyma is an outstanding feature of its strengthening system, occurring throughout the length of the plant (plate X; C, D). It is also a common structural arrangement in grasses generally. Hayward (1938) stated that stems so constructed have a "continuous zone of hypodermis variable in thickness within the epidermis and enclosing longitudinal bands of chlorenchyma". More precisely, the outer portion of such a stem consists of a parenchymatous cortex, regularly interrupted by girders of sclerotic tissue, which link peripheral bundles with the epidermis (plate X, C). Only in lower internodes do peripheral bundles become connected laterally by the sclerification of parenchyma lying between them (plate X, D). In these lower internodes the longitudinal bands of parenchyma appear to be "imbedded" in a continuous mass of hypodermal sclerenchyma, but actually, the isolation is circumscribed laterally by girder sclerenchyma and within by sclerified parenchyma. Percival (1921) stated that "a portion of the outer face of the chlorenchyma bands is always in immediate contact with the epidermis". This is true for the upper internodes of *Tripsacum* but in lower internodes the epidermis is underlain by a single layer of large hypodermal cells.

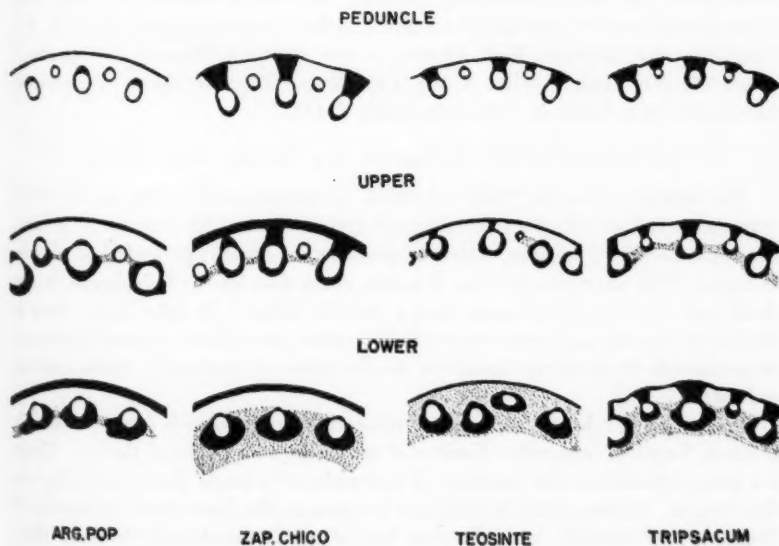


Fig. 3. Representative drawings of internodal cross-sections to show the variation in bridging within peduncle, upper internode, and lower internode in Argentine pop, Zapalote chico, Teosinte, and *Tripsacum*. Sclerotic fiber tissue in black; sclerified parenchyma stippled.

The peripheral bundles in *Tripsacum* lie close to the epidermis and their maturation in the stem either coincides with that of outer stem tissue or the procambium itself extends to the epidermis. *Tripsacum* has a rapid growth rate and at maturity consists of a relatively small number of extremely long narrow internodes culminating in an even longer peduncle (fig. 4). Maturation processes in this genus must be investigated before an attempt is made to compare its pattern of growth with maize.

In summary, the strengthening system found in the lower internodes of most maize races studied parallels the condition found in an entire Argentine pop plant. The upper internodes, however, have a structure resembling that of *Tripsacum*. Figure 3 diagrammatically represents the basic differences in bridging described in this section.

Sclerified parenchyma. In all plants examined the lower the internode the wider the zone of sclerified parenchyma. In lower internodes sclerified parenchyma forms a radially thick, sclerotic cylinder traversed by vascular bundles (plate VII, A). Higher up (approximately 8 internodes below the tassel peduncle) it is found chiefly between peripheral vascular bundles (plate VI, B; plate IX, B, D; plate X, B, D). In the fourth internode below the tassel peduncle interfascicular sclerenchyma is found only in Papago (plate VIII, A) and in the tassel peduncle sclerified parenchyma is never found (plate IX, A, C; plate X, A, C).

A high degree of intra-racial variation occurs in regard to the extent of parenchyma that becomes sclerified, however, races which consistently were weak in the development of sclerified parenchyma include Argentine pop (plate IX, B), Chapalote, and Northern flint, whereas it was always prominent in Gourdseed (plate IX, D), teosinte (plate X, B), Papago, and Zapalote chico. Its greatest development was found in *Tripsacum* (plate X, D).

THE STRENGTHENING SYSTEM OF THE LATERAL EAR SHOOT

The lateral ear-bearing shoot, or shank, is anatomically similar to the main stem except for its lack of a well-developed hypodermis and the presence of numerous small, peripheral bundles, which originate in the excessively wide leaf sheaths or husks. The very sclerotic race Zapalote chico does have a hypodermis in the shank and at maturity internodes have a smooth surface. In other races, there is little or no hypodermis present and with desiccation the collapse of parenchymatous tissue beneath the epidermis results in the formation of externally visible grooves and ridges.

In addition to sclerotic tissue, shank strength depends on such factors as length of shank, length of internodes, diameter of internodes and weight of the ear. There is a great difference in the anatomy of internodes of a single shank depending on their length. Consequently, it is difficult to compare the short shank internodes of Gourdseed, for example, with the very long shank internodes of Northern flint. Furthermore, the amount of sclerenchyma in a shank bearing a fertilized ear is much greater than in one which bears an unfertilized ear.

Vascular bundles in the shank are generally provided with a heavy sclerotic sheath, which frequently prevents crushing of vascular tissue when arching or bending occurs. The overall strength of the shank, however, depends on the strength of tissue between the bundles or the extent of ground tissue sclerification.

The races Zapalote chico and Papago, very sclerotic in respect to their stems, have a great amount of sclerified parenchyma in their shank internodes. In plants of these two races, shanks varied in length from 7–28 cm., but all were erect at maturity. Plants of the race Gourdseed characteristically have short shanks (6–16 cm.) and their internodes have a fair amount of sclerified parenchyma. Nevertheless, all shanks of this race were bent or broken due in large measure to the combination of a very heavy ear and narrow lower internodes.

Both Northern flint and Chapalote have relatively long shanks (11–32 cm.).

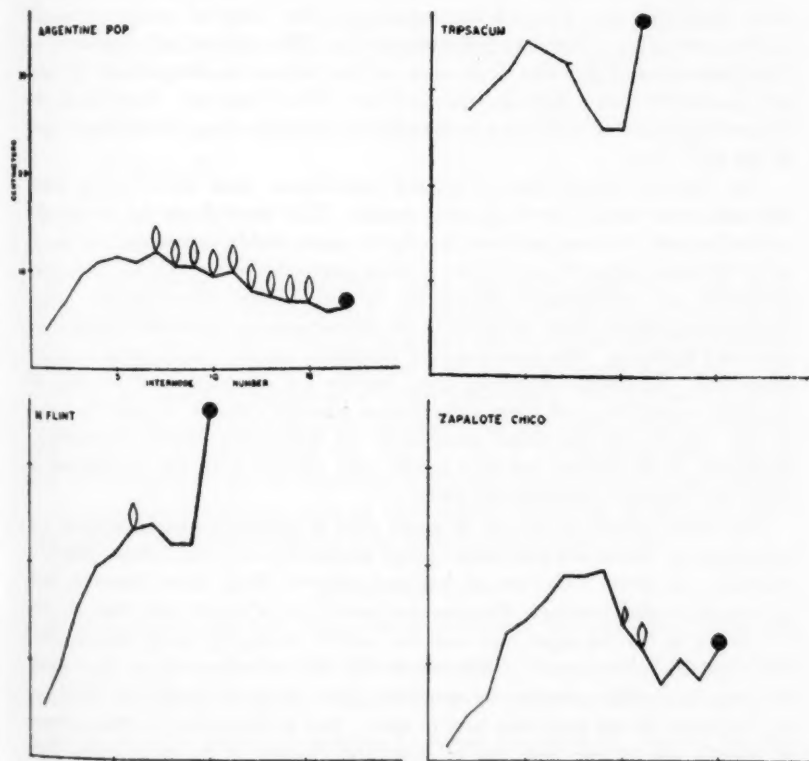


Fig. 4. Internode diagrams which typify the pattern of growth found in the races Argentine pop, Northern flint, and Zapalote chico, and the species *Tripsacum lanceolatum*.

At maturity all shanks of Chapalote plants were erect, whereas shanks of Northern flint plants were either bent or broken. The long shanks of Northern flint have few internodes and grow rapidly, while on the contrary, those of Chapalote have many internodes and a slow rate of growth. Anatomically, shank internodes of Chapalote have a wide zone of sclerified parenchyma, but there is practically none of this tissue present in the internodes of Northern flint. Since the stems of both races are quite similar in respect to sclerenchyma, the greater shank strength in Chapalote is probably due to the much longer period cells are able to deposit wall material before final maturation and desiccation.

Argentine pop has small ears borne on relatively short shanks which have many internodes, grow slowly and have fairly strong interbundle connections.

CONCLUSION

The tissue which strengthens and supports a maize stem can be subdivided into three categories: long fibers of the hypodermis; short fibers of peripheral bundle sheaths; and thick-walled, lignified parenchyma. The amount and disposition of these three tissues differs in a single stem and the manner of change from the base of a plant to its apex is dependent on the plants growth behavior. As a result, the relative importance of each tissue in contributing strength changes in different parts of the same stem.

The greatest sclerification of ground parenchyma takes place in the lower internodes—the earliest on the plant to mature. This tissue diminishes acropetally and occurs only between peripheral bundles in upper middle internodes and not at all in the tassel, peduncle and the two to three internodes below. Middle and upper internodes are strengthened principally by hypodermal sclerenchyma, which develops its greatest radial thickness in the slow-maturing internodes between ear and tassel peduncle. The importance of peripheral bundle sclerenchyma increases acropetally. In middle internodes these bundles are interconnected laterally by sclerified parenchyma and form a continuous sclerotic cylinder within the hypodermis. Higher up, the lateral connections are weaker but sheath sclerenchyma developing at the phloem end of a bundle may connect with the hypodermis or epidermis forming a subepidermal girder.

The basic growth pattern of all maize races is similar in that elongation and maturation of leaves and internodes occurs acropetally with the former generally preceding the latter. The rate of leaf maturation is fairly even, however, each successively higher internode elongates and matures at a slower rate than the one next below so that an upper internode may still be elongating while its associated leaf is already fully mature. Differences in the time of maturation of stem tissue and vascular bundles entering the stem from leaves leads to changes in the structural anatomy of the stem from base to apex. Just as races differ in their pattern of growth, the manner and time of structural changes in the stem differ from plants of one race to those of another.

A race such as Argentine pop with a uniform rate of growth shows only slight changes in its structural anatomy from one internode to the next, whereas Zapalote chico with a rapid initial growth rate, which is abruptly slowed down above the position of an ear shoot, has a corresponding sudden change in structural anatomy. Northern flint with a rather even but rapid growth rate undergoes changes similar to those in Zapalote chico but much more gradually. In the upper internodes of such a plant the length of leaves decreases along with the time of stem maturation.

The maize races studied were classified for overall scleroticness on the basis of their hypodermis, peripheral bundle sheaths and sclerified parenchyma and the result was in agreement with field observations on standability. All plants used in the present study were harvested after final maturation and desiccation, at which time it was noted if stems were standing, bent over or broken. Results of this observation are presented below.

Race	No. of plants			% plants standing	Strength of stem based on anatomy
	standing	bent	broken		
Zapalote chico	14	1	0	93%	strong
Papago	13	2	1	87%	strong
Gourdseed	11	4	0	73%	medium strong
Northern flint	10	2	3	66%	medium strong
Chapalote	8	5	2	53%	medium
Argentine pop	3	7	5	20%	weak

The introduction of teosinte germ plasm into maize reportedly leads to an increased induration of all plant parts (Mangelsdorf and Cameron 1942; Galinat et al. 1956). Teosinte plants used in the present study were not especially indurate; in fact, they were less sclerotic than most of the maize races examined. Two plants do not represent teosinte as a whole; nevertheless, they do show that the range of variation within the genus *Euchlaena* includes quite unsclerotic plants. Both species of *Tripsacum* were very sclerotic, but *T. lanceolatum* much more so than *T. dactyloides*. The arrangement of sclerotic tissue in *Tripsacum* is similar to the structure in the upper part of teosinte and most maize races but in lower internodes it is distinctly different from both *Euchlaena* and maize.

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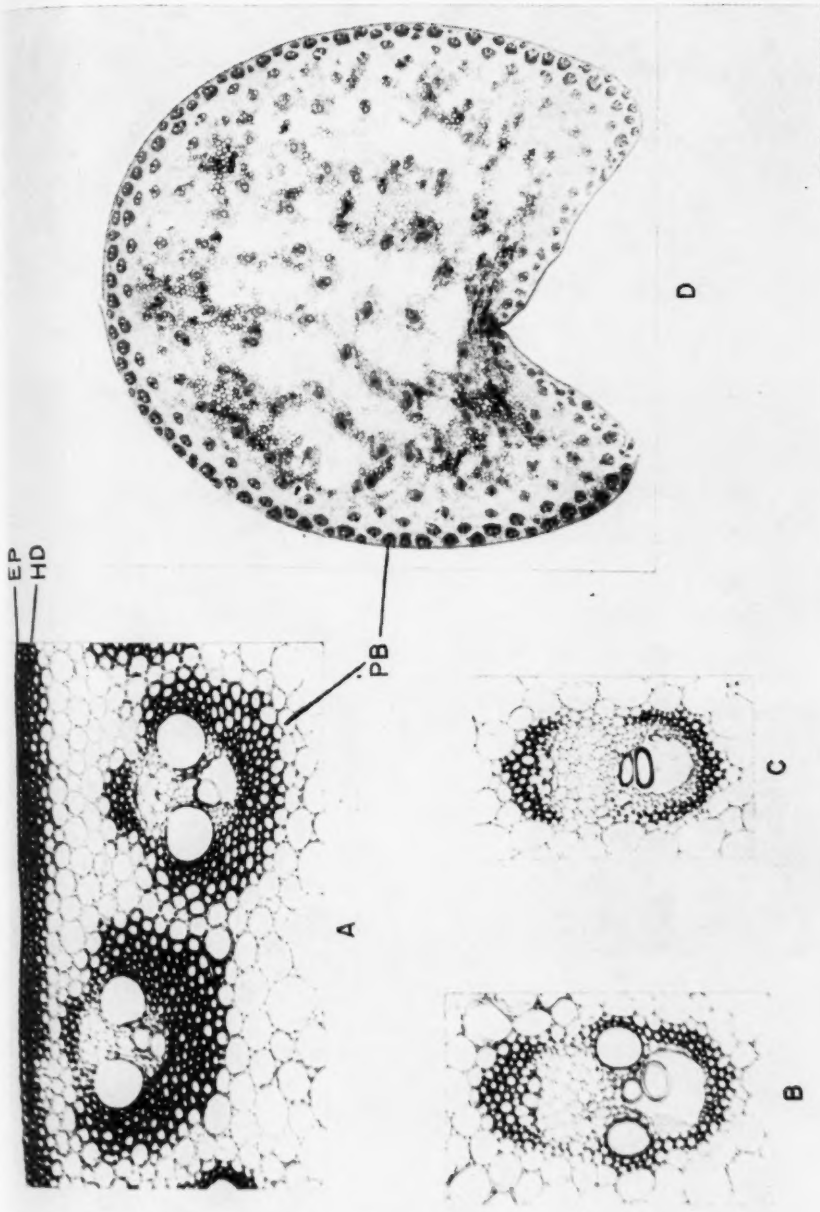
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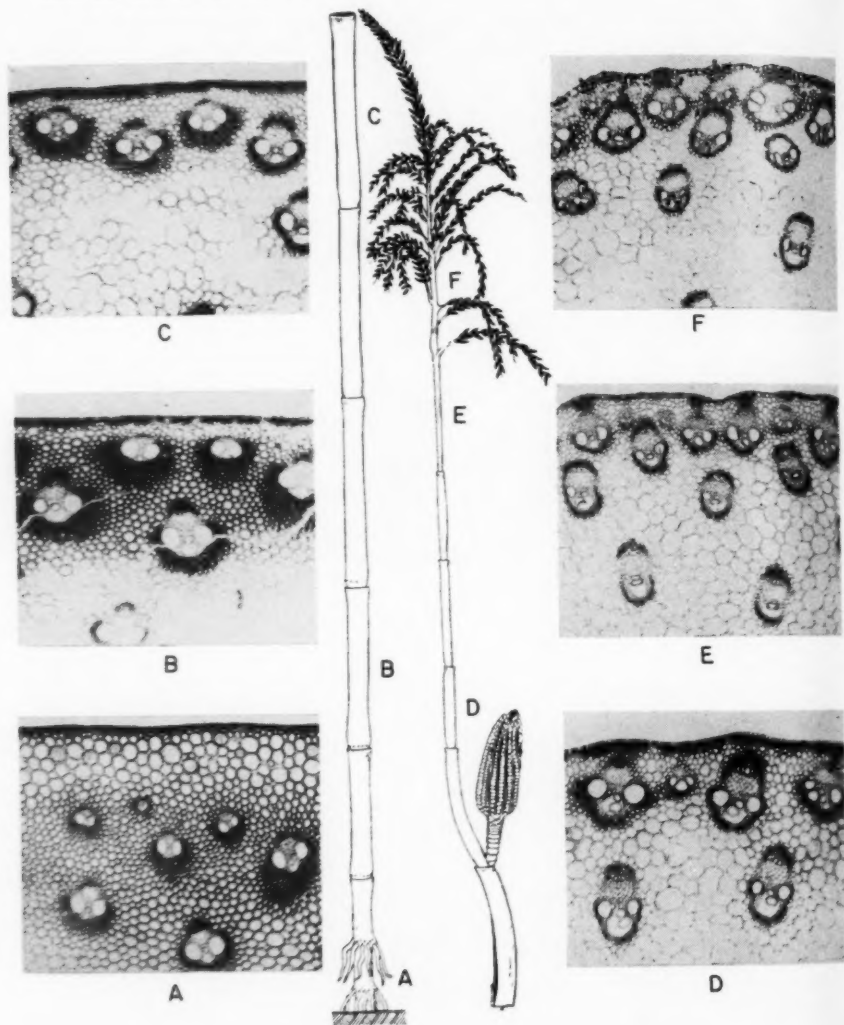
EXPLANATION OF PLATE

PLATE VI

Structural features of a maize stem. A, Transection of the peripheral region of an internode showing hypodermis (HD), peripheral vascular bundles (PB), and thick-walled parenchyma between the latter ($\times 100$). B, Transection of a vascular bundle ($\times 107$). C, An atypical vascular bundle lacking well-developed metaxylem vessels. Bundles of this kind were found in the tassel peduncles of all Zapalote plants ($\times 107$). D, Transection of a maize stem taken from a middle internode which shows the arrangement of vascular bundles ($\times 7.7$).



MURDY-STRENGTHENING SYSTEM IN STEM OF MAIZE



MURDY-STRENGTHENING SYSTEM IN STEM OF MAIZE

EXPLANATION OF PLATE

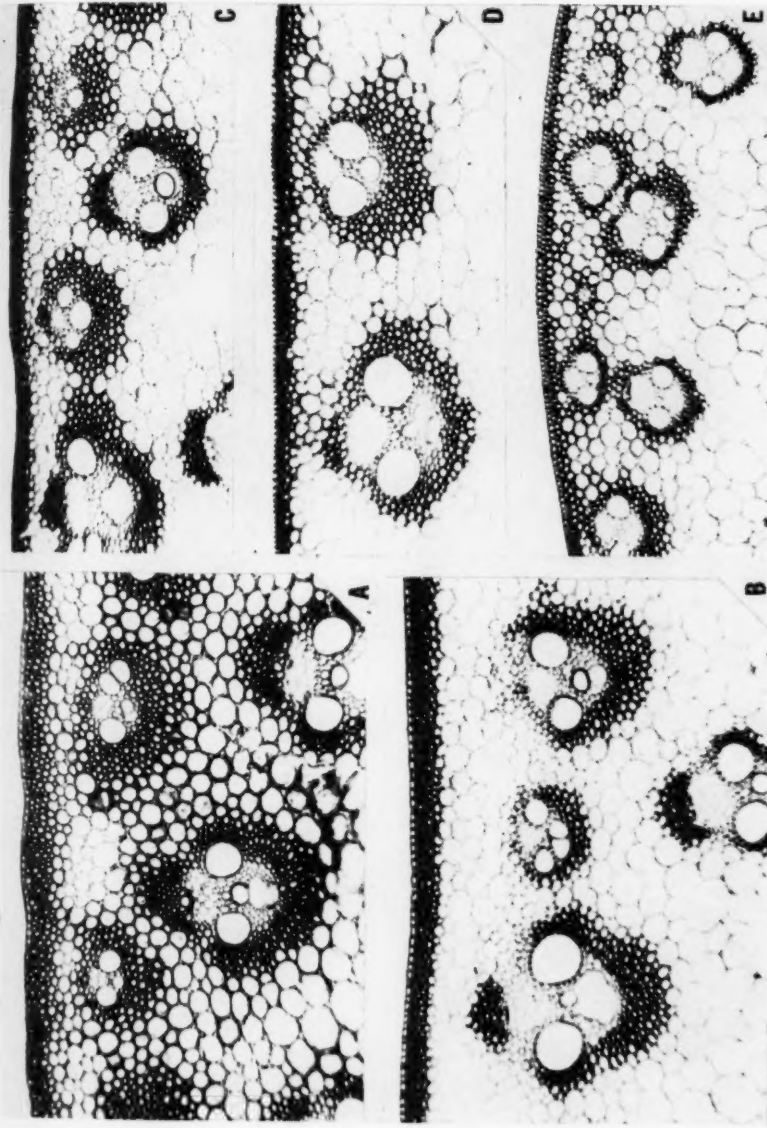
PLATE VII

Scale drawing of a completely mature Zapalote chico plant with leaves removed ($\frac{1}{2}$ natural size), and transverse anatomical sections from every third internode of this plant to show the changes in structural anatomy occurring in a single stem ($\times 35$).

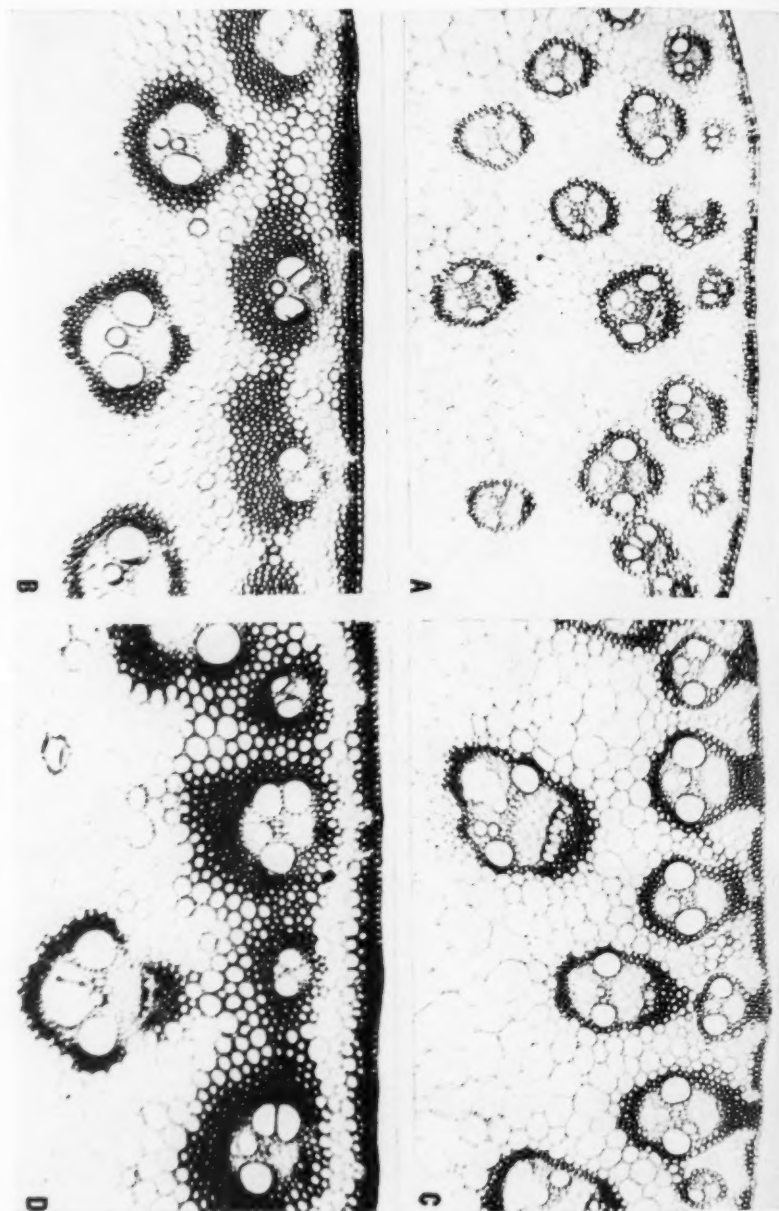
EXPLANATION OF PLATE

PLATE VIII

Transections of the fourth internode below the tassel peduncle to demonstrate racial differences in hypodermal development ($\times 70$). A, Papago; B, Gourdseed; C, Chapalote; D, Northern flint; E, Teosinte.



MURDY—STRENGTHENING SYSTEM IN STEM OF MAIZE



MURDY-STRENGTHENING SYSTEM IN STEM OF MAIZE

EXPLANATION OF PLATE

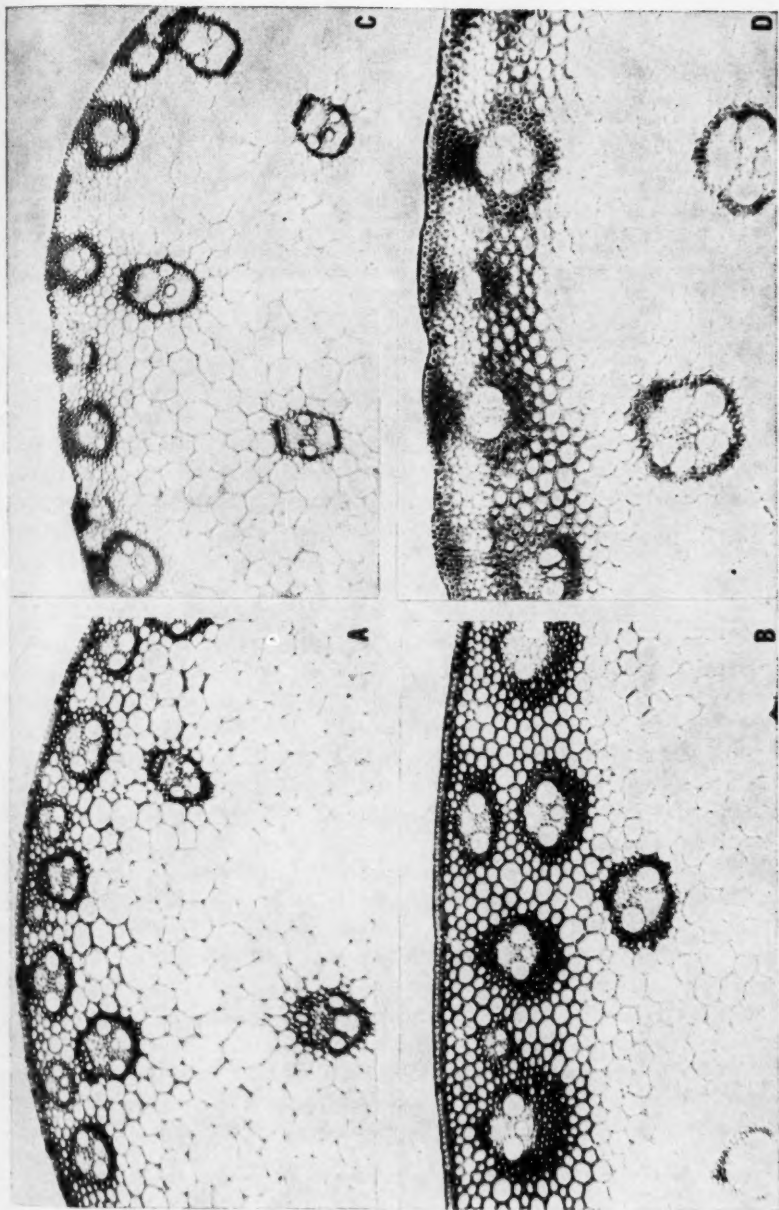
PLATE IX

Internodal transections of Argentine pop (A, B) and Gourdseed (C, D). Upper sections (A, C) made from the tassel peduncle; lower sections (B, D) taken from the eighth internode below the peduncle ($\times 70$).

EXPLANATION OF PLATE

PLATE X

Internodal transections of Teosinte (A, B) and *Tripsacum* (C, D). Upper sections (A, C) made from the tassel peduncle; lower sections (B, D) taken from the eighth internode below the peduncle ($\times 70$).



MURDY-STRENGTHENING SYSTEM IN STEM OF MAIZE

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STUDIES INVOLVING SUSTAINED TREATMENT OF MAIZE WITH GIBBERELIC ACID I: FURTHER NOTES ON RESPONSES OF RACES*

NORTON H. NICKERSON AND THOMAS N. EMBLER

ABSTRACT

Field-grown plants of four representatives of three exotic kinds of maize were subjected to four different concentrations of gibberellic acid throughout the growing season. Internode diagrams of controls and treated plants demonstrated that increases in height were taking place in different internodes under different gibberellic acid (GA) concentrations, and that related maizes responded in similar fashion to like GA treatments. General reductions were noted in tiller number, tassel branch number and ear number. High concentrations of GA inhibited growth, eventually killing plants of one race. Degree of inbreeding seems closely associated with GA sensitivity. Male sterility and production of female florets in basal areas of tassels occurred. Brace roots were formed up to 80 cm. above ground. The question of effects of GA on internal mineral balance is discussed briefly. It is suggested that the poor vegetative growth shown by maize plants under excesses of GA may be attributed to a greatly increased rate of respiration. A note of caution is sounded concerning extrapolation to other plant forms of conclusions based on behavior under GA treatment by one cultivar. NORTON H. NICKERSON, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis 10, Missouri; THOMAS N. EMBLER, Dennis-Yarmouth Regional High School, South Yarmouth, Massachusetts.

INTRODUCTION

In previously reported work (Nickerson, 1959), one hybrid, two inbreds and representatives of two exotic kinds of maize were subjected to treatment each third day with four different concentrations of GA. This paper presents results from identical treatment of four other kinds of maize which differ in their behavioral responses.

MATERIALS AND METHODS

Four kinds of maize¹ were employed in this study; they were representatives of three clearly separable races (Anderson and Cutler, 1942). A Northern Flint type (Brown and Anderson, 1947), New York Flint, was chosen to compare its behavior to that of Parker's Flint, a representative employed in the previous study (loc. cit.). Classifiable as "Southern Dent corns" (Brown and Anderson, 1948), Gourdseed (see their Plate 20) and Cherokee Dent (probably a member of their Mexican June complex; see their Plate 22) were chosen both to give a comparison between two forms whose ears were different but whose plant types were not, and to complete the study of Corn-belt ancestral types (Anderson and Brown, 1952a, 1952b) from combinations of which presumably such inbreds as L317 and CC5 investigated earlier (loc. cit.) were derived.

Two ears of Cherokee Dent, one with 12 rows and the other with 14 rows, were obtained from Henry Busby, who in 1959 was about 90 years old. He farms the upper end of an isolated valley near Pollard, Arkansas. His father was a full-blooded Cherokee Indian (or Chero-cow, according to his nephew, from whom these details came) who came from North Carolina by way of Tennessee; this strain of maize was brought to Arkansas with him and has been grown, but probably not in complete isolation, by his family since pre-Civil War times. It is the only corn

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¹Grateful acknowledgment is made to the following individuals for their cooperation in supplying seed: Dr. William H. Murdy, Department of Biology, Emory University, Atlanta 22, Georgia, for Gourdseed; Mr. Derrel Busby, Route 1, Pollard, Arkansas, for Cherokee Dent; Professor A. A. Johnson, Department of Plant Breeding, Cornell University, Ithaca, New York, for New York Flint; Dr. E. G. Anderson, California Institute of Technology, Pasadena, California, for Argentine Pop.

which the family considers fit for human consumption; this fact may have helped keep it relatively uncontaminated. The family refers to this maize as "90-day corn", and often uses it for two crops each year in Arkansas. In New England, at 41° 42' North Latitude (the equivalent of central Iowa), this maize reached anthesis in 74 days during the 1959 growing season. Fully ripened ears were harvested 35 days later, but it is not known how many days preceding actual harvest date they may have reached ripeness. Its growing season in a cooler more northerly latitude thus approximates 100 days.

A distinctive South American type, Argentine Pop, was also included. This pop corn was collected among others by Cutler in 1941 (personal communication). It has figured prominently in recent genetic work involving the reconstruction of an ancestral maize form (Mangelsdorf, 1958 a, b). According to Alava (1952), Nickerson (1953) and Anderson and Brown (1953), the original source of the strain employed in this study and used for genetical and observational work both at Johnston, Iowa, and Arcadia, California, was seed collected by Mr. Lorenzo Parodi. Plants of both Argentine Pop and Gourdseed have been studied anatomically by Murdy (1960).

In the present study, each type of maize was planted in 15-meter rows; plants were spaced about 25 cm. in the row, and rows were 1½ meters apart. In view of results obtained from randomized rows and blocks of maize in a previous study (Nickerson, 1959) there was no attempt to randomize treatments applied within each row. The total number of plants in each row was divided into five groups with as nearly equal numbers as possible, and all plants in a particular group received the same treatment. The five treatments were the same as those used before and are as follows:

- 1 — distilled water (controls)
- 2 — distilled water with 5 ppm GA
- 3 — distilled water with 25 ppm. GA
- 4 — distilled water with 125 ppm GA
- 5 — distilled water with 625 ppm GA

Every third day for the duration of treatments one ml. of the appropriate solution containing either distilled water or water plus the above-listed concentrations of GA² was applied from a pipette into the apical leaf cavity of each plant. Solutions were freshly made each time, or stored no longer than three days in darkness at 19° C. Insects (corn borer and corn earworm) were controlled by hand removal and by a weekly dusting of 5% DDT ("Neudust") beginning when evidence of infestation was first noted (July 10) and continuing until elongation ceased and pollination had occurred. Fertilizer (Agrico 5-10-10) was applied at the rate of 700 lbs./acre three and six weeks after germination. Planting date was June 12, 1959; treatments began July 6 and continued until tassel emergence (Table 1).

² The GA employed was kindly supplied by Dr. Curt Leben, Agricultural Research Division, Eli Lilly and Company, Greenfield, Indiana.

RESULTS

Initial response in all forms was rapid. Two days after the first treatment had been applied, plants in all treated groups showed increases in height; these ranged up to twice the heights of control plants. During the next two weeks, controls underwent little or no internode elongation; analysis of mature treated plants (Fig. 1) shows that early internode elongation was greatly enhanced by GA, provided that the internode tissue had not reached its final stage of differentiation by the time of treatment. An attempt was made to record the sixth node on each plant by counting all leaves from the coleoptile up (but not the coleoptile itself) when the plants were young. This fifth leaf was known from previous observations to be present on mature plants. It was marked by clipping a metal staple into the leaf. Small arrows on the internode diagrams (Fig. 1) show these sixth nodes as they were determined by fifth-leaf attachment when the plants were mature.

As a precaution against wind damage, many of the rows were staked and plants tied to lines beginning during the fifth and sixth week and continuing throughout the growing season.

New York Flint. (Tables 1, 2, 6; Fig. 1). Higher treatments of 125 and 625 ppm tended to increase lengths of internodes below the ear most drastically; even though upper internode lengths were less than those of the lower internodes in these plants, they were still equal to or greater than upper internode lengths in control plants. Just as noted in the previous study on the closely related Parker's Flint, the 125 ppm treatment proved most detrimental, and there was a recovery toward normal by plants treated with the higher 625 ppm doses. Ear production on plants treated with 125 ppm doses was much lower than with all other treatments. Ears produced by plants treated with 625 ppm doses were much shorter and smaller than those produced by controls, but kernels were set. Tillering was inhibited entirely by treatments of 25, 125 and 625 ppm. The average number of tassel branches was markedly reduced from 15.8 on controls to 6.2 on plants treated with 125 ppm doses. Plants receiving 625 ppm doses produced nearly twice this minimum number, but their average of 11 branches was still only $\frac{2}{3}$ the number produced on control plants. Tassels were exerted within 2-3 days in all groups, but anthesis was first noted in plants treated with 25 ppm doses.

Leaves averaged 7 cm. at their widest point on controls. On plants receiving 5 ppm doses, leaves averaged 5 cm. in width and were generally longer by 15 cm. than the same leaves on controls compared just before tassel emergence. Plants treated with 25 ppm doses had at this time leaves as wide as controls but again longer by 15 cm. In plants receiving 125 ppm treatments culm diameter was only half that of control plants; leaves were no longer than control plants, and they averaged only 3 cm. in width at their widest points. The 625 ppm treatments produced plants with quite thin culms (5-10 mm.), long internodes, and compared with controls, much narrower and shorter, occasionally rolled leaves. These rolled leaves were noted previously on plants which were eventually killed by an overdose of GA (Inbreds L317 and CC5; Nickerson, 1959); their rolling may be described

as epinastic with relation to the midrib rather than with relation to the culm, in that the upper epidermis seems to grow more rapidly than the lower to the extent that a tubular structure is formed. A picture of this bizarre feature is shown (for Argentine Pop) in Plate XI. Tassels of these plants all produced female caryopses, but in only two of the four saved for study were these functional. These female spikelets were produced along the basal portions of branches and central spikes.

Brace roots were not formed as copiously on these plants as on Parker's Flint, but primordia did appear as high as 30 cm. above the ground. Their total growth averaged 2-4 cm. Tassel height was significantly increased in plants receiving 5, 25 and 125 ppm doses; it was decreased in plants receiving 625 ppm doses.

Gourdseed. (Tables 1, 3, 6; Fig. 1). All plants treated with GA showed initial responses in height. Plants treated with 5 ppm doses were definitely more vigorous than controls. This vigor was first manifested in increased height; plants 6 weeks old averaged 45-60 cm. compared with an average height of 30-36 cm. for controls. This effect persisted through to maturity. Leaf number (13-14) at 6 weeks was the same for controls, 5 ppm and 25 ppm-treated plants, but with 5 ppm treatments, leaf blades were 10-15 cm. longer than the 75-90 cm. average lengths on controls; leaf blade width at widest point averaged 7-9 cm. compared to the 6-8 cm. average of control plants. The average number of ears and of primary tassel branches showed increases with both 5 ppm and 25 ppm doses compared with controls. Although plants treated with 25 ppm doses reached greater average heights than did those treated with 5 ppm doses, they were not as vigorous as controls. Culms were slightly smaller, and leaves all averaged 6 cm. in width. On plants treated with 125 ppm doses, ear number was not reduced compared to controls, height was not increased over treatments using 25 ppm and primary tassel branch number was reduced only slightly compared to controls. Total tassel height was also about equal to that of controls. Leaves were equal to controls in length, but averaged only 3-5 cm. in width and were easily broken.

Plants treated with 625 ppm doses showed a marked height increase compared to controls; this increase was attributable entirely to greater elongation of lower internodes. Culms however were thinner; leaves averaged only 2-3 cm. wide and were easily broken. Ear number was reduced, tassel height was reduced approximately 14% and the area over which tassel branches arose was greater by 40% when compared to controls. At 11 weeks of age, tassels had fully emerged in all other plants, but not in this group. When they emerged, 3 out of the 5 tassels collected for study had some well-developed caryopses in basal areas of branches and central spikes. In these areas, sessile spikelets were always female and pedicellate spikelets were always male. Of the five tassels, one with caryopses and one with no caryopses were male sterile. Pollen shedding, therefore, was apparently not dependent upon the presence or absence of caryopses in the tassel.

Brace root formation in control and 5 ppm-treated plants was confined to the lower node or two exclusively; in plants treated with 25 ppm doses, they arose on the lower 3-4 nodes. The same number of nodes formed brace roots in plants

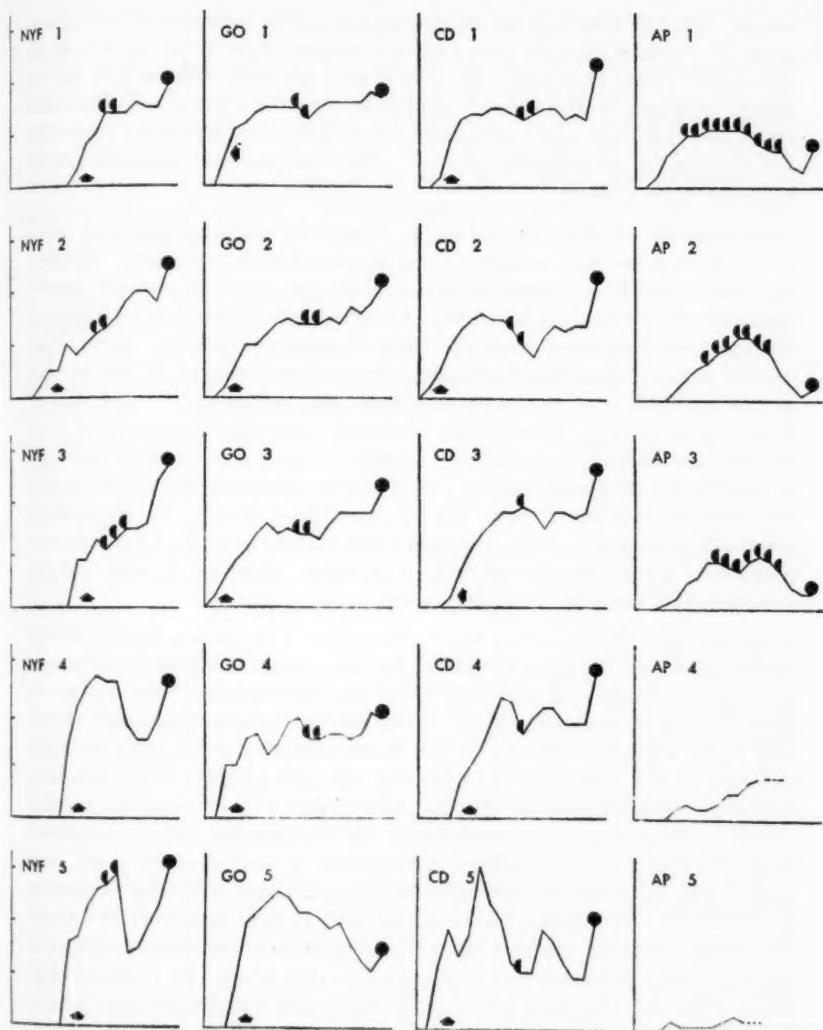


Fig. 1. Internode diagrams of control (top row) and GA-treated maize plants. Horizontal axis is internode number. Vertical axis is internode length; each division is 10 cm. Circle denotes tassel, semicircle denotes ear; arrow depicts node of attachment of fifth leaf above coleoptile.

NYF, New York Flint; GO, Gourdeed; CD, Cherokee Dent; AP, Argentine Pop.

Number 1 stands for distilled water treatments (controls); 2 for 5 ppm GA; 3 for 25 ppm GA; 4 for 125 ppm GA; 5 for 625 ppm GA. Further explanation is given in the text.

treated with 125 ppm, but the extreme lengths of the internodes in this group meant that some of the brace roots were initiated more than 40 cm. above ground. These roots seldom grew more than 3 or 4 cm., and many were only 1 cm. in length. In plants treated with 625 ppm doses, there were consistently five nodes visible on which brace roots had initiated. Root length was also seldom more than 3-4 cm., and for the majority was 1 cm. They were, however, produced as high as 80 cm. above ground.

Cherokee Dent. (Tables 1, 4, 6; Fig. 1). This maize resembled Gourdseed rather closely in responses and appearances of treated and untreated plants. Greatest responses occurred in younger plants; as plant size increased, recovery toward appearance of control plants was noted. Greatest height increase was with doses of 125 ppm; relatively little effect was noted on most measurements except when doses of GA applied contained 625 ppm. At that level, number of ears, number of primary tassel branches, length of central spike and peduncle length showed decreases over the same measurements in controls; only the area over which tassel branches arise showed an increase over controls. Tassels of these plants, however, did not develop any female spikelets. Bending over occurred when the plants were 6-9 weeks of age in the 125 ppm- and 625 ppm-treated groups. The phenomenon occurred in rapidly elongating internodes 1 meter above ground. Such bent-over stalks could not be straightened without breakage. One control plant had the only two tillers observed in this population.

Argentine Pop. (Tables 1, 5, 6; Fig. 1; Plate XI). This race was highly sensitive to all doses of GA. In plants 6 weeks of age, those receiving 5 ppm doses averaged 20-30 cm. in height compared with 15-20 cm. for controls. They had 10-11 leaves visible compared to 8-9 leaves on controls. Tiller number of plants treated with 5 ppm doses was also reduced; at 6 weeks, controls had 2-3 tillers per plant and those treated with 5 ppm doses had only one tiller per plant. This difference was less at maturity, however. Among plants treated with 25 ppm, tiller number and ear number were both reduced below the corresponding values for control plants. A few silks were produced in basal areas of tassel branches and central spikes. Also, leaf width was reduced by half from averages of 5-7 cm. in controls to 2.5-3.5 cm. At 6 weeks, plants treated with 25 ppm doses were 30-37 cm. tall. Plants receiving 125 ppm doses of GA were nearly all eliminated by the treatment; some plants, however, persisted longer than others. At 6 weeks of age, 10 out of 22 plants had been killed; at 11 weeks, only 5 were surviving, and two of these had been mutilated by wind. This mutilation was likely attributable to the extremely brittle nature of these plants. Under doses of 625 ppm, plants showed a strong initial response, but at 6 weeks of age only 8 out of 22 were alive, and at 11 weeks, only one plant was alive. This latter plant was not more than 5 cm. above ground, and its stem was highly contorted (Plate XI). Both doses of 125 and 625 ppm produced plants with thin leaves. In one 125 ppm-treated plant, they were in addition so inrolled that their tips never became free; a "ladder" effect was thus obtained (Plate XI). This plant produced a tassel, never exerted, which was female below and male above; it also lacked tassel branches (Plate XI).

DISCUSSION AND CONCLUSIONS

This study, along with the previous one (Nickerson, 1959), reinforces the point that the effects of GA on maize are marked, but dependent upon both the race studied and the concentration of GA employed. Internode diagrams (Anderson and Schregardus, 1944) for the four maizes studied were constructed as before, being in each case in Fig. 1 that of an actual plant which best represented its group of five plants studied. These diagrams were constructed from the tassel down, hence the internodes were drawn in the inverse order of their appearance, and tassels are at the same relative position on each graph.

New York Flint and Cherokee Dent show the same pattern of internode elongation above the points of ear attachment. Gourdseed and Cherokee Dent, however, show a much greater similarity with regard to internodal development below the point of ear attachment. Argentine Pop, because of the large number of ears formed, is not comparable to any of the other races. Its growth pattern is here the same as that reported for it by Murdy (1960) under growing conditions in Iowa: the first three internodes are increasingly longer, a plateau is then reached followed by a gradual decline in successive lengths until the longer peduncle is developed.

Vertical comparison of these graphs within each column shows what concentrations of GA affected which internodes within each race of maize: horizontal comparisons show how the various races responded to the same concentrations of GA.

In New York Flint, 5 ppm and 25 ppm treatments produced growth patterns generally alike, affecting most of the internodes above the point of ear insertion. Arrows indicate the point of attachment of the 5th leaf at the top of the fifth internode. The coleoptile is not here counted as the first leaf. Extra internodes were consistently formed below points of ear attachment on plants treated with 125 and 625 ppm GA. An extra internode appears in the diagram of the 5 ppm-treated plant above the point of ear attachment. This observation was true for 4 of the 5 plants measured. Possibly low concentrations of GA applied early enough delay formation of inflorescence primordia for a time. This suggestion is in line with findings of Bradley and Crane (1960) on *Prunus* sp. cultivars, where GA prevented initiation of floral primordia but did not interfere with production of bud-scales.

A comparison between diagrams of New York Flint and Parker's Flint of the previous study (loc. cit.) shows a general similarity of curvature, including the anomalous detrimental behavior under treatments of 125 ppm. The fact that New York Flint plants treated with 5 and 25 ppm doses exhibit less departure from the control growth pattern than do plants of Parker's Flint treated with these same doses may be interpreted as signifying that New York Flint has in its genetic makeup some other maize germ plasm and is not therefore as "pure" a representative of Northern Flint as is Parker's Flint.

Gourdseed shows remarkably little internodal pattern change under doses of 5,

25 and 125 ppm compared with controls; under treatments of 625 ppm, its curve is quite similar to that for 125 ppm-treated New York Flint. These results may likewise be interpreted as indicating that Gourdseed is in itself not a "pure" representative of its race, Southern Dent; its hybrid ancestry, referred to by Brown and Anderson (1948), has apparently buffered its protoplasmic reactions to GA. This same situation may be seen in the previous experiments (loc. cit.) with regard to Spancross, a known hybrid. In fact, in its general slight effect on 5, 25 and 125 ppm-treated plants, and its stimulation of early internodes followed by declines in length except for the peduncle, GA creates much the same effect on both Gourdseed and Spancross. The general beneficial effect of low doses of GA on Gourdseed have been alluded to above; it is possible that GA may find commercial importance in boosting yields on maize strains which are strongly of Southern Dent ancestry.

Gourdseed also has much in common with the internode pattern of Zapalote Chico, a race also previously studied (loc. cit.). The two maizes respond nearly alike to treatments with 5 ppm and 25 ppm doses; with the higher concentration of 125 ppm, Zapalote Chico shows more sensitivity to GA than does Gourdseed. When the GA concentration was highest (625 ppm) their developmental patterns were again strongly similar.

Cherokee Dent, based on its lower row number and less conspicuous denting, is also a representative with mixed genetic background. This contention is borne out by relatively slight differences in internode patterns of controls, 5, 25 and 125 ppm treatments. There are also strong resemblances between its responses and those of both Gourdseed (see above) and Zapalote Chico of the previous study (loc. cit.). Brown and Anderson (1948) mentioned that the Southern Dents were a variable lot and that on both cytological and morphological evidence they showed a strong affinity to the dent corns of central Mexico. This contention was accepted fully by Wellhausen et al. (1952). In their general internode patterns of control plants and in their similar responses to various doses of GA, these resemblances are further confirmed.

Argentine Pop, as it is grown in the United States, is known to be a highly inbred race. Two sorts, based on plant height and ear size, were segregated out of the original collections independently in studies conducted at Johnston, Iowa, (Edgar Anderson, personal communication) and at Arcadia, California, (E. G. Anderson, personal communication). Cutler (personal communication), who has collected and observed Argentine Pop in its native range in South America, regards it as being essentially inbred there also. He also reported the taller, fewer-eared segregants as not being "uncommon". This race may therefore be considered to be a rather pure one. The present study, however, used material which for several generations has always produced small ears in large numbers. Ears of this distinctive race have been figured by Weatherwax (1954, fig. 59) and Mangelsdorf (1958 a, b; fig. 6).

In its strong sensitivity to GA, Argentine Pop resembles responses of the inbreds

CC5 and L317 studied previously (loc. cit.). Higher doses are fatal; in Fig. 1, the only survivors of the 125 ppm and 625 ppm groups are graphed simply to show the extent to which deleterious reactions may go and still allow the plant to remain alive. These two plants were collected and later photographed (plate XI). The well-documented effects of GA on reduction of tiller number and ear number were also graphically illustrated (table 5). Tassels of 25 ppm-treated plants developed a few silks and female spikelets; the one non-exserted tassel of the 125 ppm-treated survivor showed a completely female basal portion and a male but sterile tip portion (Plate XI). Its general resemblance to a basal immature inflorescence is remarkable.

It may therefore be concluded that GA affects maize in a fashion depending directly upon the degree of inbreeding or homozygosity of the strain involved. Since there are now many forms of maize, and since they exhibit a vast range of human control or lack of it over their past pollinations, it seems reasonable to conclude that responses of no one form of maize are "standard".

It is precisely because of such racial or varietal differences that generalized conclusions, especially where a variable cultivated plant is used as experimental material, must be based upon wide studies. As an example one might compare the explanation offered for the predominant way in which GA acts in plant elongation by Feucht and Watson (1958) with that of Greulach and Haesloop (1958). The former workers, using the cultivar Blue Lake of *Phaseolus vulgaris*, concluded that cell elongation was primarily responsible for GA-induced increase in internode length. The latter workers, using the cultivar Black Valentine of *Phaseolus vulgaris*, concluded that only cell division was responsible for GA-induced increase in internode length. Paleg and Aspinall (1958) reported differences in response to GA under the same environmental conditions in two varieties of barley. Kline (1959), working with celery plants, showed that age of plant was also important in eliciting a particular response. He suggested it may be more important even than dosage of GA applied. Other examples might also be cited; these instances referred to above, however, reinforce the argument for caution in extrapolative interpretation of results.

The rather marked increase in length of peduncles in most treated groups (Fig. 1; Table 6) as well as a general increase in height of tassels (Table 6) are likely attributable directly to the influence of GA on these parts when the plant is quite young. Murdy (1960) has pointed out, as has Kiesselbach (1949), that the peduncle and tassel of maize mature relatively early at a time when internodes below are still immature.

The thin culms and general lack of vigor in maize plants treated with high doses of GA may be a direct result of higher-than-normal respiratory rates. Using wheat seedlings, a 20% rise in respiration under treatment with GA has been reported by Luštinec and Krekule (1959). Coulombe and Paquin (1959), working with tomato, reported rapid increase in respiration, photosynthesis and transpiration with a peak 5-6 hours after treatment, followed by a rapid decline, but higher respiration and photosynthesis rates than controls during limits of their experiment. Ormrod and Williams (1960) found that plants of *Trifolium birtum*

showed a striking increase in acid soluble phosphorus and decrease in inorganic phosphorus as quickly as one minute after treatment with GA. Using bean plants, Linck and Sudia (1960) showed that GA-treated plants absorbed more P^{32} than did controls. There thus may be a correlation between GA treatment, respiratory rate and phosphorus metabolism.

The phenomenon of poor leaf separation, noted occasionally in all forms given higher treatments with GA in both this study and the previous one and illustrated by Plate XI, resembles illustrated symptoms of calcium deficiency (Hambidge, 1941). Went (1957) similarly noted this same "harp-like" structure on corn plants grown under continuous light.

The brittleness of maize plants treated with higher concentrations of GA may be because of mineral imbalance within the plant. In carnations, Laurie and Kiplinger (1948) reported that overdoses of potassium will cause brittleness and snapping off at nodes. Whether the GA-induced aberrations in mineral content of maize plants also causes a potassium imbalance resulting in brittle stems and leaves is not known. It may only be concluded that overdoses of GA apparently upset mineral balances in plants.

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TABLE 1

TOTAL AMOUNT OF GA RECEIVED BY EACH PLANT IN MICROGRAMS

	No. of Treatments	Amount of GA per treatment				
		0	5	25	125	625
New York 8-rowed Flint	15	0	75	375	1875	9375
Gourdseed	18	0	90	450	2250	11250
Cherokee Dent	15	0	75	375	1875	9375
Argentine Pop	19	0	95	475	2375	11875

TABLE 2—NEW YORK FLINT

Treatment in ppm of GA		0	5	25	125	625
Averages of 3 plants in each treatment group	Height (nearest cm.)	126	164	170	233	204
	Number of Nodes	10	12	11	11.25	10.75
	Number of Tillers	2.6	2.6	0	0	0
	Number of Ears	2.0	2.0	2.2	0.25	0.75
	Number of Primary Tassel Branches	15.8	11.8	12.6	6.2	11
	Percent of Tassels Wholly Male Sterile	0	0	0	100	100
	Percent of Tassels with some Functional Pistillate Florets	0	0	0	25	75
Original Size of Population		17	17	17	18	18
Number Surviving		16	16	17	13	11
Number of wind-damaged plants among survivors		0	0	0	3	7

TABLE 3 — GOURDSEED

Treatment in ppm of GA		0	5	25	125	625
Averages of 5 plants in each treatment group	Height (nearest cm.)	211	220	243	243	262
	Number of Nodes	15.2	15.4	16.8	15.6	15.6
	Number of Tillers	0	0	0	0	0
	Number of Ears	1.4	2.2	1.6	1.4	0.8
	Number of Primary Tassel Branches	12.4	14.6	13.0	11.8	11.8
	Percent of Tassels Wholly Male Sterile	0	0	0	0	40
	Percent of Tassels with some Functional Pistillate Florets	0	0	0	0	60
Original Size of Population		25	21	23	23	24
Number Surviving		25	20	23	22	24
Number of wind-damaged plants among survivors		0	0	0	10	12

TABLE 4 — CHEROKEE DENT

Treatment in ppm of GA		0	5	25	125	625 (3 plants)
Averages of 5 plants in each treatment group	Height (nearest cm.)	218	233	235	275	255
	Number of Nodes	15.8	16.6	15.8	15.2	16.4
	Number of Tillers	0.2	0	0	0	0
	Number of Ears	2.2	2.2	1.8	2.0	0.6
	Number of Primary Tassel Branches	21.8	25.6	23	18.8	16
	Percent of Tassels Wholly Male Sterile	0	0	0	0	30%
	Percent of Tassels with some Functional Pistillate Florets	0	0	0	0	100%
Original Size of Population		17	18	18	18	17
Number Surviving		14	17	18	17	13
Number of wind-damaged plants among survivors		0	0	3	7	10

TABLE 5 — ARGENTINE POP

Treatment in ppm of GA		0	5	25	125	625
Averages of 5 plants in each treatment group	Height (nearest cm.)	101	87	83 (3 plants)	46	Insuff. No. of Plants
	Number of Nodes	14.2	13.4	15.2	13.0	Insuff. No. of Plants
	Number of Tillers	4.2	3.0	1.2	0	Insuff. No. of Plants
	Number of Ears	7.6	7.6	5.8	0	Insuff. No. of Plants
	Number of Primary Tassel Branches	22.4	21.6	20.8	No tassels exerted	
	Percent of Tassels Wholly Male Sterile	0	0	0	No tassels exerted	
	Percent of Tassels with some Functional Pistillate Florets	0	0	0	No tassels exerted	
	Original Size of Population in Each Treatment Group	23	22	22	22	22
Number Surviving		23	17	14	5	1
Number of wind-damaged plants among survivors		0	0	3	2	0
Number of plants dying from treatment		0	5	8	17	21

TABLE 6
5-PLANT-AVERAGE LENGTHS OF CERTAIN MEASUREMENTS
CONTRIBUTING TO HEIGHT

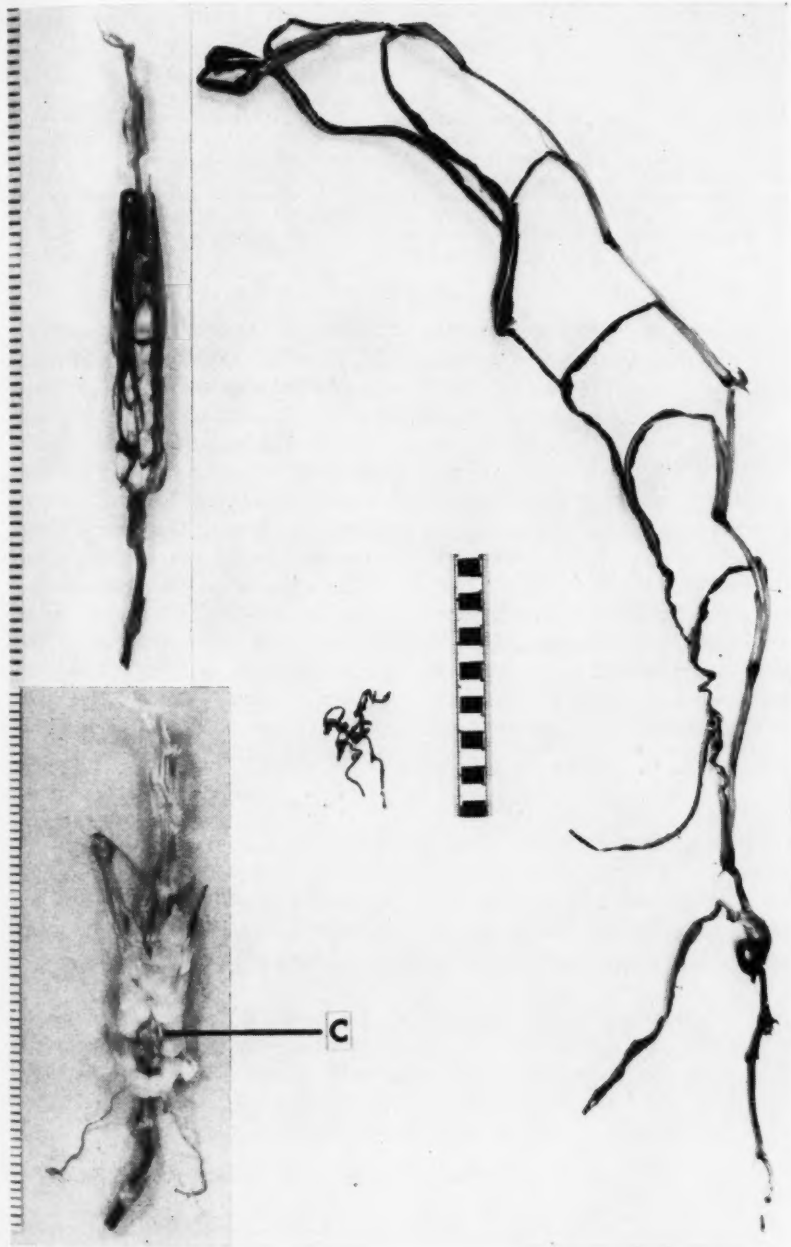
Treatment of GA in ppm.		0	5	25	125	625
Central spike length (cm.)	New York Flint	24.0	31.8	27.5(4)*	31.0(2)	10.0(4)
	Gourdseed	24.0	23.6	24.8	21.2	18.6
	Cherokee Dent	26.6(3)	23.0	28.2(4)	24.0(4)	19.6(3)
	Argentine Pop	17.8	19.0(4)	19.4	—	—
Branching area below central spike (cm.)	New York Flint	11.4	10.2	15.2	14.8(4)	13.2(4)
	Gourdseed	10.4	12.4	12.8	14.0	11.8
	Cherokee Dent	15.6	17.4	16.8	16.2	18.3(3)
	Argentine Pop	9.0	8.6	7.8	—	—
Peduncle length (cm.)	New York Flint	17.2	24.2	28.2	25.8(4)	21.8(4)
	Gourdseed	19.0	19.0	17.4	18.6	11.8
	Cherokee Dent	23.0	21.0	24.6	22.4	14.0(3)
	Argentine Pop	5.0	2.8	2.8	—	—
Tassel height (branching area plus central spike of tassels in cm.)	New York Flint	35.4	42.0	42.7	45.8(4)	23.2
	Gourdseed	34.4	36.0	37.6	35.2	30.4
	Cherokee Dent	42.2	40.4	45.0	40.2	37.9(3)
	Argentine Pop	26.0	27.6	27.2	—	—

* Numbers in parentheses refer to number of plants from which measurements were made when 5 plants were not available.

EXPLANATION OF PLATE

PLATE XI

Argentine Pop. Plant on right treated with 125 ppm GA each three days for entire growing season. Note ladder-like effect of leaves joined at tips. Bulge at top containing small ear photographed at extreme left; top photo is dry ear, while lower photo is same ear gently boiled in water and partly dissected. Note male spikelets at top, paired female spikelets (2 silks at base of lower left-hand photograph indicate one pair) and lack of tassel branches. Well-developed cupules are also found on this tassel; line marked C indicates one in oblique view. Plant in center is contorted culm and leaves of only surviving maize plant in group receiving 625 ppm GA. Brace roots were thin, brittle and poorly developed on both plants. Black and white checked ruler divisions are 1 cm. each; fine divisions are 1 mm. each.



NICKERSON & EMBLER—GIBBERELIC ACID TREATMENT I

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STUDIES INVOLVING SUSTAINED TREATMENT OF MAIZE WITH GIBBERELIC ACID II: RESPONSES OF PLANTS CARRYING CERTAIN TASSEL-MODIFYING GENES*

NORTON H. NICKERSON

ABSTRACT

Plants containing each one of seven different tassel-modifying genes were treated with Gibberellic Acid-distilled water mixtures every three days throughout the growing season until tassel emergence. GA was found to suppress expression of *ramosa-1* (*ra*₁). Tassel-seeds 2 (*ts*₂), 5 (*ts*₅) and 6 (*ts*₆), Tunicate (*Tu*) and Vestigial glume (*Vg*) were all modified, but not so much that they could not be recognized. The recessive male-sterile 1 (*ms*₁) remained male-sterile. An explanation of certain elongation patterns in these plants is tentatively made, which points toward the idea that GA depends at least in part on the presence of auxin (IAA) for its effects. NORTON H. NICKERSON, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri.

INTRODUCTION

Phinney (1956) showed that *dwarf-1*, a recessive maize mutant, responded to Gibberellic Acid (hereinafter called GA) in such a way as to become phenotypically normal with a total amount of 60 micrograms of GA applied regularly during the growing season. Recently (Nickerson, 1960a) it has been shown that the dominant maize genes Corn-grass (*Cg*) and Teopod (*Tp*) likewise respond to sustained GA treatments in a like manner, becoming essentially normal in phenotype. It has also been shown previously (Nickerson, 1959; Nickerson and Embler, 1960) that normal maize plants respond to sustained treatment with GA in several characteristic ways. Inasmuch as some of the growth manifestations noted under such GA treatment resembled some known tassel mutants, it was decided to grow obtainable seed of a series of tassel mutants previously studied (Nickerson and Dale, 1955) and subject them to various strengths of GA treatment throughout their growing seasons. The maize mutants¹ Tassel-seed 2 (*ts*₂), Tassel-seed 5 (*ts*₅), Tassel-seed 6 (*ts*₆), Vestigial glume (*Vg*), Tunicate (*Tu*), *Ramosa-1* (*ra*₁) and Male-sterile 1 (*ms*₁, later shown to be identical to tassel-seed 8 of Nickerson & Dale, 1955) were grown, treated and studied.

MATERIALS AND METHODS

Planting distances and cultural methods employed are the same as those set forth in an earlier account (Nickerson and Embler, 1960). There were generally 2 or 3 lots of seed available for each of the above-listed mutants. Each of the stands of plants resulting from these seed lots was divided into four groups with as nearly equal numbers as possible; all plants in a particular group received the same treatment.

Concentrations of GA chosen were in the range shown by a previous study (Nickerson, 1959) to have a detectable but not drastic effect on field-grown maize plants. The four treatments employed were as follows:

- 1 — distilled water (controls)
- 2 — distilled water with 50 ppm GA

* This work was supported by a grant from the National Science Foundation.

¹ Thanks are hereby gratefully extended to Dr. Earl B. Patterson, Department of Botany, University of Illinois, Urbana, Illinois, for providing seed from Maize Genetics Cooperation sources for this study.

3 — distilled water with 100 ppm GA

4 — distilled water with 150 ppm GA

Each third day for the duration of treatments one ml. of the appropriate solution containing either distilled water or water plus the above-listed amounts of GA² was applied from a pipette into the apical cavity of each plant. Solutions were freshly made each time, or stored no longer than three days in darkness at 19° C. Planting dates, beginning treatment dates, ending treatment dates, total numbers of plants grown and total amounts of GA applied to each mutant are shown in Table I.

RESULTS

Tassel-seed 2 (ts₂). Seed stocks employed had no normal sibs. Because of the extreme general uniformity of plants within each treatment group, measurements were made only on four single treated plants exhibiting the mutant form (Table II). Central spike length was generally decreased with increasing dosage, as were the number of primary tassel branches, the area over which they originated, and the number of ears produced. Peduncle length was about equally decreased by all three dosage levels of GA. Internode number was hardly influenced at all. Plant height showed increase with GA treatment; each group of treated plants in the field was highly uniform in total plant height, but internode diagrams (Fig. 1) show that early-formed internodes were increasingly lengthened by increasing doses of GA, while later-formed ones became much shorter than those of the distilled-water-treated mutant plant. Specimen tassels show a rapid decrease in overall size, but proportions of peduncle length, branch number, spikelet number and caryopsis development remain relatively constant (Plate XII).

Tassel-seed 5 (Ts₅). Plants were either normal (+/+) or heterozygous (Ts₅/+) in genetic constitution. Figures listed under "M" on Table II are averages for 4 mutant (Ts₅/+) plants; figures listed under "C" are measurements for the single control (+/+) plant in that group. Length of central spike was depressed solely by doses of 100 ppm GA in mutant-carrying plants; only slight changes were manifested in normal sibs. Tassel branch numbers fluctuated with no definite pattern in treated mutant-carrying plants; a consistent reduction was noted by all strengths of GA employed on normal sibs. The length of stem over which tassel branches developed was relatively consistent for both mutant-carrying and normal sibs regardless of GA concentration employed. Peduncle length of normal sibs was relatively uniform, but 50 ppm doses of GA tended to shorten this length somewhat in mutant-carrying plants, while 150 ppm doses tended to lengthen peduncles by about the same amount. Internode number increases consistently in mutant-carrying plants with increasing dosage; in normal sibs the number is uniformly increased by all GA levels employed. Ear number is increased in both mutant-carrying plants and normal sibs by doses of 50 ppm GA; further increase in GA dosage level does not decrease ear number in mutant-carrying plants, but drastically does so in normal sibs.

Plant heights of mutant-carrying plants, nearly equal to those of normal sibs

² The GA employed was kindly supplied by Dr. Curt Leben, Agricultural Research Division, Eli Lilly and Company, Greenfield, Indiana.

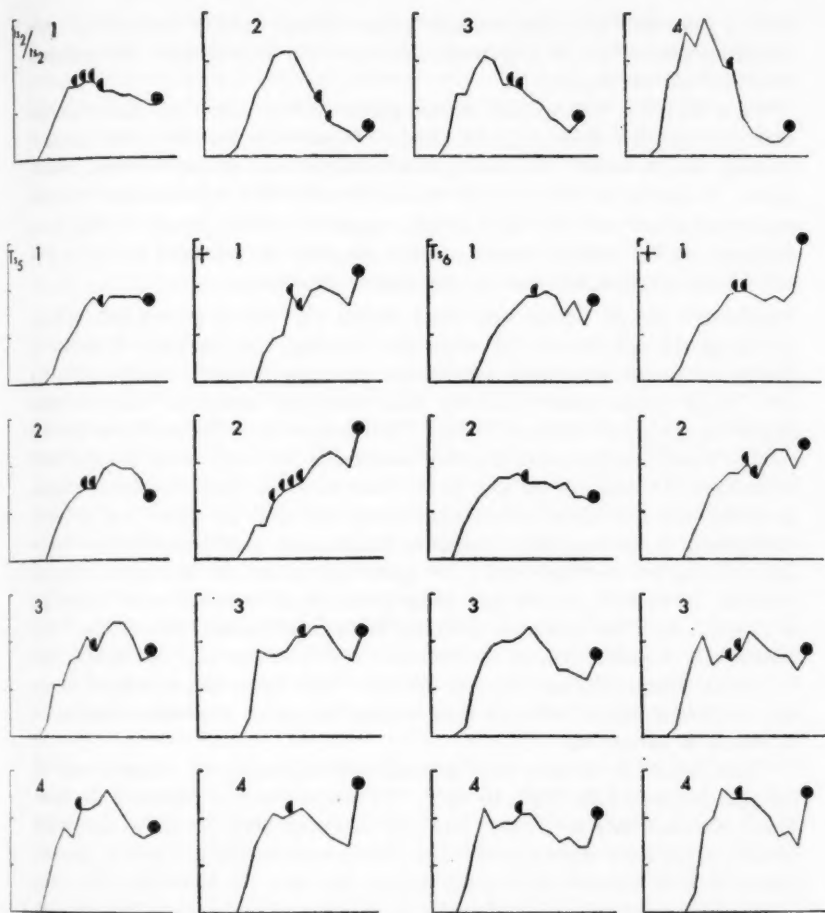


Fig. 1.

Figs. 1-3. Internode diagrams of various maize plants with either normal or mutant conditions showing responses to treatment with GA. Numbers are indicative of treatments, as follows: 1, distilled water; 2, 50 ppm GA; 3, 100 ppm GA; 4, 150 ppm GA. Internode lengths are indicated in 10-cm. units on ordinate; internode number may be determined from the abscissa. These graphs were all plotted from the tassel down, so all tassels (dots) are in the same relative position on each graph. Ears are represented as semicircles.

under control (H_2O) doses, are not as sensitive as those of normal sibs until the GA dosage reaches 150 ppm. Analysis of internode diagrams show that peduncle lengths in normal sibs are as long or longer than the longest lower internodes. The consistent dip below the peduncle and above the ear is present in all cases. With increase in dosage, early-formed internodes become longer. Mutant-carrying plants

show a different form from normals under control (H_2O) treatments; with increasing doses of GA, it is the internodes above the ear and below the peduncle which become the longest.

Plate XIII, No. 1 shows both control plants (left of ruler) and plants treated with 150 ppm GA doses (right of ruler). Normal sibs are above and mutant-carrying sibs are below. Increased peduncle lengths may be seen on both treated plants. Reduction in tassel branch number in normal sibs is prominent; branches on treated plants are also more loosely organized. More female florets were developed on GA-treated mutant-carrying sibs than on untreated controls, but GA did not stimulate formation of caryopses in normal sibs.

Tassel-seed 6 (Ts_6). Plants were either normal (+/+) or heterozygous ($Ts_6/+$) in genetic constitution. As with the foregoing, "M" in Table II refers to averages of measurements made on 4 mutant individuals while "C" refers to values for a single normal plant under the same treatment condition. Central spike length was not greatly decreased by any GA treatments in either mutant or normal forms. Tassel branches, however, were consistently increased in the mutant with increasing GA concentration and at the same time decreased in normal plants. Branching area was increased in mutants with increased GA doses, but did not vary greatly in normal plants. Peduncle lengths were greatly modified by lower doses of GA, but the high level (150 ppm) approached the average of control mutants. In normals, the 100 ppm dosage produced the most noticeable depression in length, a fact also consistent with the behavior of normal sibs of Ts_5 . Ear number was in general reduced by treatment with GA, but only the highest dose (150 ppm) affected the normal sib in this way. More internodes on mutant plants seem to have elongated with GA than without it, but no consistent trend could be noticed in normal sibs.

Plant heights of mutants were increased with increasing GA dosage; doses of 150 ppm increased total height by 50%. By contrast, normal sibs with the same dosage increased only by 11%. Internode diagrams (Fig. 1) show that with distilled water, lower internodes are about the same in length and general gradual increase in both mutant-carrying and normal sibs; it is the internodes above the ear which account for their differences in height. 50 ppm treatments seem to stimulate all internodes about equally, except for a reduction in peduncle length of the normal sib. 100 ppm of GA has a greater stimulation of lower internodes but apparently tends to shorten all upper internodes. 150 ppm doses on both mutant-carrying and normal sibs show a marked effect on the early internodes with a peak length reached below the ear; each internode is then shorter up until the peduncle, which although long, does not exceed the longer internode. A comparison between these last curves shows a considerable amount of similarity.

Plate XIII, No. 2 shows tassels from mutant-carrying and normal sibs. Those on the left of the ruler received treatment with distilled water; those on the right with 150 ppm GA. Peduncle growth in mutant-carrying plants is notable, reduc-

tion of silks and increase in stiffness of branches are likewise easily seen. Some female florets are developed at the base of the normal sib's branches and central spike; its reduced branch number can also be seen. No developed kernels have been found in any of the 15 control mutant-carrying tassels studied. In those treated with 150 ppm GA, several normal-sized caryopses were noted in three out of four tassels. These caryopses always were in the same basal locations at which caryopses develop in normal sibs under this same treatment.

Vestigial glume (Vg). Plants were either normal (+/+) or heterozygous (Vg/+). In Table III, "M" refers to average measurements of 4 mutant-carrying plants and "C" to measurements of single normal sibs. Central spike length was reduced but not consistently by GA in both mutant-carrying and normal sibs. Tassel branch number was increased by 50 ppm doses on mutant-carrying plants and decreased by both 100 and 150 ppm doses. On normal sibs, tassel branch number was reduced consistently by all GA doses. Tassel branching area for both mutant-carrying and normal sibs showed little or no response to GA. Peduncle length was reduced by 50 and 150 ppm GA treatments in mutant sibs; in normals, both 50 and 100 ppm GA treatments caused reductions, but 150 ppm doses resulted in a peduncle length close to that of the distilled water-treated plant.

Ear number was generally increased on mutant-carrying plants with increased GA concentration; ear number on normal sibs was increased by doses of 100 ppm GA, but doses of 150 ppm GA completely inhibited ear formation. Numbers of elongated internodes were increased by GA in mutant-carrying sibs by all concentrations of GA; approximately the same results were noted in normal sibs.

Plant heights were adversely affected in both groups by 50 ppm GA doses; in normal sibs, 100 ppm doses produced even shorter plants, while 150 ppm doses produced the tallest plants. In mutant-carrying sibs, an adverse effect is also noted by 50 ppm GA doses, but 100 ppm doses produced a greater average height than doses of 150 ppm. Internode diagrams (Fig. 2) show similar curves for both mutant-carrying and normal sibs. Doses of 50 ppm GA markedly depress elongation of internodes above the ears and do not influence internode length below the ears. With doses of 100 ppm GA early-formed internodes are greatly elongated and later-formed ones even more drastically reduced. Curves for plants which have been subjected to doses of 150 ppm GA show that internodes immediately below sites of ear formation are most greatly stimulated in elongation while those immediately below the peduncles are most strongly inhibited in elongation.

Plate XIV, #1 is of normal sibs (upper tassels) and mutant-carrying sibs (lower tassels) of plants treated with distilled water (left of ruler) and 150 ppm doses of GA (right of ruler). Tassel branch reduction under GA treatment is apparent. Shortening of the mutant-carrying peduncle by GA may also be seen. Production of female caryopses (florets) does not occur in either normal sibs or mutant-carrying plants with this dosage; a very few are developed at the base of the lowermost tassel branch under 100 ppm doses in both mutant-carrying and normal sibs.

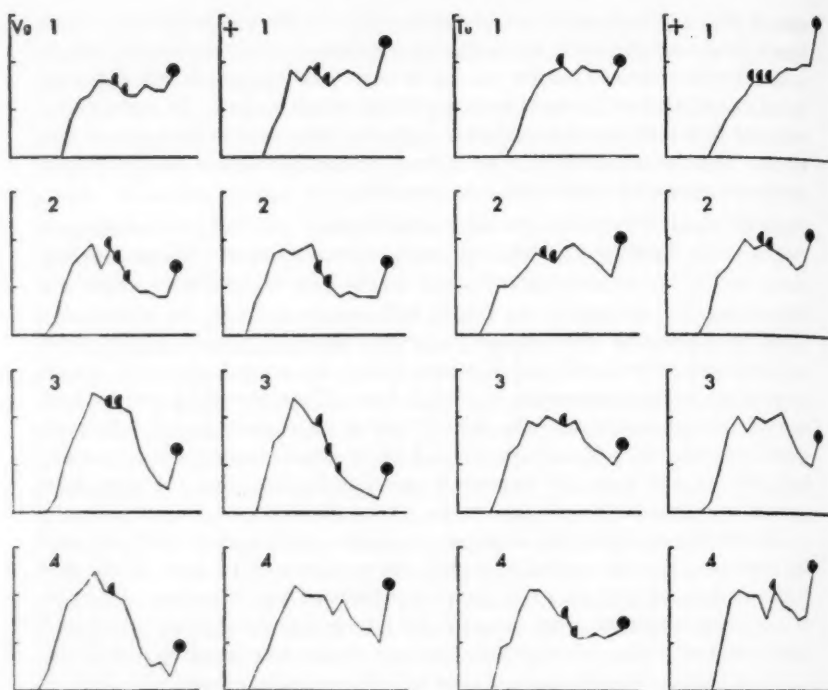


Fig. 2.

Tunicate (Tu). Plants were either normal (+/+) or heterozygous (Tu/+) in genetic constitution. Column "M" in Table III is based on average measurements of 4 mutant-carrying plants, while column "C" figures are for single normal plants. Central spike length is increased in mutant-carrying sibs by doses of 50 and 100 ppm GA. In normal sibs, no reduction in length is noticed until doses reach 150 ppm; this highest dose also shortens central spike length of mutant-carrying sibs, but not as profoundly. Tassel branch numbers are decreased by about half by all doses of GA in mutant-carrying plants; 50 ppm and 100 ppm doses on normal sibs cause great reduction, but 150 ppm doses seem to have little effect. The length of culm over which branches arise is not changed much on both mutant-carrying and normal sibs by any treatments, except that 50 and 100 ppm doses on normals apparently cause some reduction. These two dose levels likewise cause a reduction of peduncle length in normal sibs. Peduncle length in mutant-carrying plants is noticeably decreased only by doses of 150 ppm GA. Ear number is relatively constant for all mutant-carrying sibs, but increased dosages cause decreases in ear formation on normal plants. Internode number of normal sibs is

actually reduced slightly by doses of 150 ppm GA; this same dosage causes more internodes to elongate in mutant-carrying sibs.

Plant heights of normal sibs are not altered significantly by any GA treatments; increases in heights of mutant-carrying sibs were obtained with doses of 50 and 100 ppm, but 150 ppm treatments produced plants whose average lengths were shorter than those of plants subjected to the lower concentrations. Internode diagrams (Fig. 2) show that while normal sibs treated with distilled water show generally increasing internode lengths from base to peduncle; 50 and 100 ppm GA treatments tend to elongate lower internodes and shorten upper internodes. Doses of 150 ppm GA tend to make all internodes long. In mutant-carrying plants, internodes above the ear tend to remain the same length as in water-treated plants. Doses of 50, 100 and 150 ppm progressively make lower internodes longer and upper internodes shorter.

Plate XIV, #2 shows tassels from normal and mutant-carrying sibs. Those treated with distilled water are left of the ruler; those treated with 150 ppm doses GA are at the right. Normal sibs are uppermost, mutant-carrying sibs are lowermost. Reductions in tassel branch number are apparent. Development of silks and large glumes at bases of branches of mutant-carrying sibs are seen. The shorter peduncle is also prominent.

Ramosa-1 (ra_1). Crosses were made so that plants were either heterozygous ($+/ra_1$) or homozygous (ra_1/ra_1) in genetic constitution. In Table III, column "M" represents average measurements of four homozygous plants; column "C" figures are for single heterozygous plants. Central spike lengths were not greatly altered in either homozygous or heterozygous plants, except for some increases in both plant types under doses of 100 ppm GA. 50 ppm doses of GA reduced tassel branch number in heterozygous but not in homozygous sibs. 100 ppm doses were not as effective on heterozygous sibs as were 50 ppm doses, but on homozygotes, a marked reduction of branching was obtained. 150 ppm doses were as effective as 100 ppm doses on heterozygotes, but on homozygotes a reduction in average branch number of more than 50% resulted. The length of culm over which these branches arise was affected by doses of 150 ppm only. This same dosage increased the length in heterozygous plants and decreased the length in homozygous sibs. The final result in each case was nearly identical, a fact borne out by the two tassels on the right in Plate XV, #1. Average peduncle lengths did not differ with treatment in homozygotes, but with heterozygotes, an apparent reduction under 100 ppm doses and 33% increase under 150 ppm doses was obtained.

Ear number in homozygotes was generally reduced by GA treatments, but ears were still the highly branched forms typical for ra_1 (Nickerson and Dale, 1955). The reduction was greatest with 150 ppm GA doses, but all strengths did cause a decrease. In heterozygotes, all GA treatments caused a consistent amount of reduction. Internode number in homozygotes was apparently increased most by doses of 50 ppm GA; higher concentrations reduced this number, but it remained higher than the average for control (water-treated) plants. 100 ppm doses

affected heterozygotes greatest; a reduction below the number present in controls was noted at the 150 ppm level.

GA increased plant heights of homozygotes in a linear relationship to dosage; with the exception of 150 ppm doses, heterozygotes behaved the same way. Even this latter plant, however, was $\frac{1}{3}$ higher than its sib which received only distilled water. Internode diagrams (Fig. 3) show that the general pattern exhibited by water-treated homozygotes of increasing internode length up to the ear and further increases for each internode above the ear were simply accentuated for all levels of GA dosage employed. Heterozygous sibs show the same basic pattern with water treatments, with 50 ppm doses and, with some deviation, with 150 ppm doses. Doses of 100 ppm, however, apparently caused many of the internodes produced above the ears to be generally shorter (with one glaring exception) than those preceding them.

Plate XV, #1 shows tassels of heterozygous (upright) and homozygous plants (inverted). The two on the left were treated with distilled water; those on the right with 150 ppm GA. Note reduction in tassel branch numbers and increase in peduncle lengths. Female caryopses were nearly non-existent, on either hetero- or homozygotes.

The strong resemblance of both treated homozygous and heterozygous tassels to control tassels of $+/+$ plants in Plate XIV should be noted.

Male-sterile 1 (ms_1). Plants were either heterozygous ($+/ms_1$) or homozygous (ms_1/ms_1) in genetic constitution. In Table III, "M" columns are average measurements of four mutant-carrying plants and "C" columns are measurements for single heterozygous normal sibs. Central spike lengths of heterozygous plants were decreased by increasing doses of GA; treatments of 150 ppm caused a 27% decrease. Central spike lengths in homozygous sibs were stimulated by doses of 50 ppm GA, but 100 ppm and 150 ppm doses caused only slight variations from lengths attained by control (water-treated) plants. Tassel branch number, tassel branch area and peduncle length were generally unaffected in both homozygous and heterozygous plants by all GA dose levels; the single deviation in this pattern was the heterozygote under 150 ppm doses, where a 50% reduction in branch number was obtained. Ear number was not reduced in homozygotes except under doses of 100 ppm GA; heterozygotes showed an increase over the control under doses of 50 ppm GA but with higher doses, ear number remained unchanged from that of the control plant.

Internode number of heterozygotes seemed to be increased slightly by 50 and 100 ppm doses. Homozygotes showed a definite increase in number of measurable internodes over control plants with all GA treatment levels.

Plant heights of homozygotes were increased by 50 and 100 ppm doses, but 150 ppm doses did not increase them further. Heterozygotes were relatively unchanged by all GA levels except 150 ppm which caused about a 10% increase in height. Internode diagrams (Fig. 3) show that heterozygotes have a series of internodes that increase rather rapidly and then form a relatively flat plateau with

a slight increase in the peduncle. 50 ppm doses of GA affect later-formed internodes so as to give a series of continually longer internodes from base to tassel. 100 ppm doses increased earlier internode lengths over those shown in controls. 150 ppm doses exaggerated early internode lengths and shortened later ones up to the peduncle, which is about as long as that of the control plant. Curves for homozygotes carrying the mutant show strong similarity in control plants to heterozygotes. 50 ppm doses show no marked changes, but 100 ppm doses tend to accentuate lengths of early internodes and shorten lengths of later-formed ones. This trend is even more pronounced under doses of 150 ppm. The general curve produced is quite similar to that produced by the heterozygote under similar treatment.

Plate XV, #2 shows tassels from heterozygous (upper) and homozygous (lower) plants. Two are from plants treated with distilled water (left of ruler) and two from plants treated with 150 ppm GA (right of ruler). The general reduction in tassel branch number and wider spacing of spikelets on branches is apparent. However, no pollen was shed by homozygotes treated with GA. Three female caryopses with silks were developed at the base of the lowest branch of one mutant-carrying tassel in the five which were collected. Their development in other tassels not harvested was just as scarce.

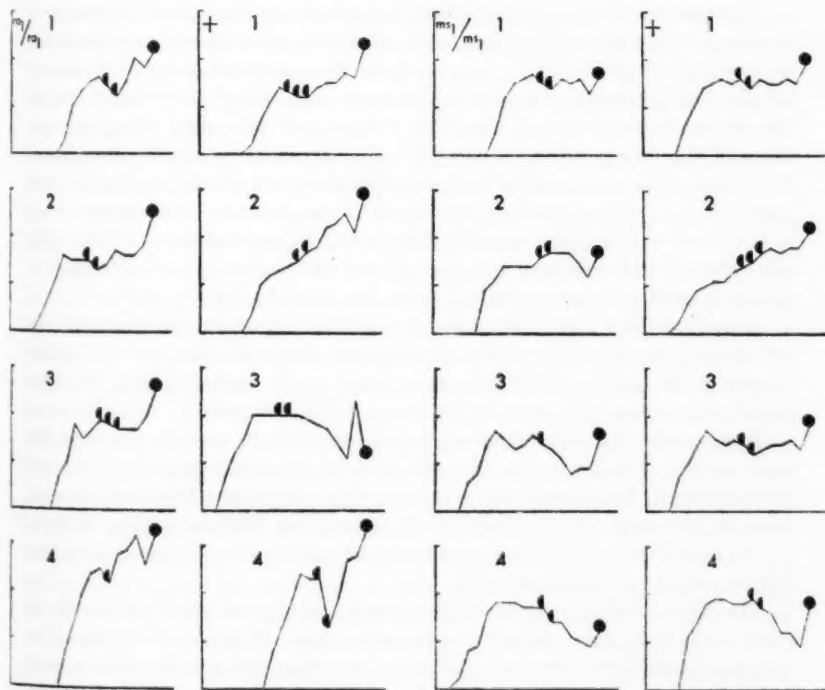


Fig. 3.

DISCUSSION AND CONCLUSIONS

Nickerson and Dale (1955) described certain morphological characters of sixteen tassel mutants. Some of these have been subjected to treatments with GA; it is planned to treat the remainder during the 1960 growing season.

Plants with genotype ts_2/ts_2 showed no lessening of the gene expression under treatment with GA, but tassels were smaller with increased doses. Expression of Ts_5 was essentially the same under GA treatment. The gene Ts_6 showed several changes in many measurements under GA treatment; resemblances of the tassel in Plate XIV, #2 to untreated ts_4 (Nickerson and Dale, Plate 24, Fig. 2) is remarkable. This gene, however, still is not modified to produce a "normal"-looking or standard tassel under GA treatment.

The genes Vg and Tu are somewhat opposite in their effects on glume growth. GA reduces their expressions somewhat, so that treated plants have many more normal-appearing glumes than untreated plants. GA-treated Vg and Tu tassels, however, did not produce much pollen. This male-sterility effect was earlier noted on normal maize plants treated with GA (Nelson & Rossman, 1958; Nickerson, 1959). Female caryopses were regularly produced in tassels with each of these genes under GA treatment.

The gene ra_1 seems to respond rather completely as far as tassel expression is concerned to GA treatment so that tassels of treated plants closely resemble tassels of normal plants (Plate XV). Ears of ra_1 in this experiment remained characteristically multi-branched structures. This result may be explained simply because GA effects do not last more than 2 or 3 days, and once tassel emergence had occurred GA treatments were stopped. The ear develops mostly after tassel emergence. This fact, coupled with the point that since plants continually grew larger and each cell was therefore proportionately less influenced by successive doses of GA, tended to keep the ears relatively free from any influence of GA. The main effect of GA seen here is apparently the well-known one of restriction of axillary branching in intact plants, a point first noted by Brian (1957).

In male-sterile 1 (ms_1), microspores abort, according to Singleton & Jones (1930) and Emerson *et al.* (1935). GA does not restore the ability of these plants to form pollen grains. Before discussing these results further, a basis for their possible explanation may profitably be introduced at this point.

It is possible that GA depends at least in part for its growth effects on the auxin supply. The maize gene *lazy* (la), known to produce quantities of auxin (van Overbeek, 1938) responds strongly to GA treatment (Nickerson, 1960b). Brian and Hemming (1958), Kuse (1958), Galston and Warburg (1959), Wareing (1958) and Weijer (1959) have all postulated a positive auxin-gibberellin relationship in a variety of plants and plant parts.

The effects of GA on these maize mutants may depend upon the amount of auxin in the plant part affected at a particular time. If it may be assumed that developing male florets produce auxin in an increasing rate which reaches a peak and then drops off rapidly shortly before anthesis, and that developing female

florets produce far greater quantities much quicker, and for a longer time but later in the life of the plant, then one could postulate the following relationship. As the tassel of a normal (+/+) plant begins its development, the peduncle receives elongation stimulus (auxin) in greatest quantity first. However, the amount of auxin produced by the tassel quickly reaches the level above which stem elongation ceases. Thus the peduncle matures early (Murdy, 1960), and the lowermost internodes elongate and mature from the base up as the auxin concentration from above rapidly increases and then decreases. The ear-shoot (an axillary bud) is stimulated by the high point of auxin concentration reached; it then begins to develop and forms silks rapidly. About the time silks are extruded, the auxin supply from the tassel diminishes toward zero. Under the influence of a diminishing auxin supply, the internodes below the peduncle but above the ear, heretofore inhibited by a high auxin concentration, finish their elongation and mature. Brace roots develop at the lower end of the culm, again as the auxin supply falls below the optimum for stem growth. Shortly thereafter, the pollinated ear produces quantities of auxin which quickly results in an excess over optimum for either stem or bud development; the internodes of the ear shoot or shank thus do *not* elongate. In many forms, the shank never fully matures, producing a structure which bends easily under the weight of the developed ear.

There are, then, the following general patterns of growth which conform to the above hypothesis concerning auxin concentrations and GA effects. Tassel-seed 2, normally a producer of quantities of female caryopses in the tassel, has its lower internodes longer than those of normal plants and its upper ones shorter than those of normal plants. In Tassel-seed 5, the first third of tassel florets differentiated are female (bases of central spikes and lower tassel branches) and all later-formed ones are male. In Tassel-seed 6, the reverse is true; the first third of spikelets in the same tassel locations are male and all outer (and later) ones are much-proliferated short branches of poorly-developed female florets.

Gibberellic Acid treatment accelerates both the early rise and the later dip in ts_2 (Fig. 1). Presumably auxin concentration rapidly reached inhibitory levels for stem elongation. In Ts_5 , the rise in lengths of internodes in control plants is followed by a leveling-off (Fig. 1); subsequent GA treatments accentuate the lengths of those internodes above the ear, formed when most auxin was produced by male florets. Peduncle lengths (here formed under amounts of auxin from female florets) were always shorter than these elongated upper internodes. In Ts_6 , (Fig. 1) a long peduncle and a steep rise in early internode length (formed under amounts of auxin from male florets) was always followed by a decline in length of internodes above the ear (formed under amounts of auxin from female florets) in control plants. GA accentuates the early rise but does not affect the decline pattern above the ears except to make all internodes slightly but uniformly longer. In Vg , (Fig. 2) an internode length is reached rapidly which decreases only slightly with a slight increase in the peduncle length. The effect of GA is to accentuate the early increase and cause marked declines in internode lengths above

the ear, with the earlier-formed peduncle length showing a final strong increase. Since the stamens of Vg dry out and die before anthesis, the late supply of tassel auxin is presumably cut off. *Tu* (Fig. 2) follows the same pattern but GA effects are less pronounced. *Ramosa-1* (*ra*₁, Fig. 3) has an internode pattern of general increase in length from base to tip; here all florets remain male, but they are quite numerous and shed pollen over a much longer period than do normal plants. GA treatment accentuates this pattern but preserves its general form.

In *ms*₁ (Fig. 3) a sharp initial increase in internode length is followed by leveling-off with only a slight dip before the peduncle. GA accentuates both the early rise and the late dip. The fact that microspores form but then degenerate before anthesis with possible consequent severe decrease in tassel auxin production would account for the GA behavior if it depended upon auxin concentration for its elongation effects.

Confirmation of many points in the above discussion must occur before it will satisfy critical investigators. It may, however, be suggested that not only does GA apparently depend upon the presence of auxin for its elongation effects, but it also depends upon the particular concentration of auxin (and GA) available in the elongating cells. A possible point in favor of this hypothesis is that it seemingly explains the effect of GA upon the dwarf gene *nana* (*na*₁); Phinney (1956) reported it as "not responding to GA treatments". Van Overbeek (1935) had previously shown that although *nana* made even more than normal amounts of auxin, the material was destroyed before it diffused down the culm. If there were no auxin, then GA, which presumably depends upon its presence for at least part of its effects, would cause no such effects. There are some facets of GA effects not explained by this proposal, but elongation effects in maize may reasonably be regarded in this manner.

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TABLE I
PLANTING AND TREATMENT DATA OF SEVEN MAIZE MUTANTS

Mutant	Planting Date (1959)	Date of first GA treatment	Total number of plants treated	Date of last GA treatment	Total number of treatments	Total Amounts of GA applied in micrograms		
						50 µg per dose	100 µg per dose	150 µg per dose
ts ₂	15 June	6 July 1959	86	14 August 1959	fourteen	700 µg	1400 µg	2100 µg
Ts ₀	16 June		104					
Ts ₆	16 June		96					
Vg	14 June		107					
Tu	14 June		126					
ra ₁	12 June		87					
ms ₁	15 June		117	26 August	18	900 µg	1800 µg	2700 µg

TABLE II
RESULTS OF GA TREATMENT ON CERTAIN MEASUREMENTS OF THREE MAIZE TASSEL-SEED GENOTYPES AND THEIR NORMAL SIBS

Genotype	Dosage of GA in micro-grams	Length of central spike (cm.)		Number of primary tassel branches		Length of tassel branching area (cm.)		Pedicule length (cm.)		Plant height (cm.)		Number of internodes		Number of ears	
		M	C	M	C	M	C	M	C	M	C	M	C	M	C
$M = t_2/t_2$ (single plant measurements)	0	27		15		10		11		171		14		4	
	50	16		12		8		5		182		15		2	
	100	20		8		8		7		182		15		2	
	150	12		13		5		5		203		15		1	
$M = T_0/+$ (av. of 4) $C = +/-$ (single plant measurements)	0	26.5	26	11	21	8.5	13	15	22	168	172	11.5	11	1.2	2
	50	30.5	30	6	14	7	14	11.5	26	177	202	12.5	13	2	4
	100	18	28	12	14	10.5	13	14.2	21	205	236	12.5	13	1.7	1
	150	27	24	8	14	7.5	15	18.5	26	240	231	13	13	2.2	1
$M = T_0/+$ (av. of 4) $C = +/-$ (single plant measurements)	0	12	35	15	14	10.2	13	25	29	167	225	13	14	1.2	2
	50	9.5	27	16	13	11	13	12	23	202	226	15	13	0.5	2
	100	9.5	32	18	8	15	10	14	17	217	241	15.5	15	0.5	2
	150	11	27	21	9	15.5	16	21	24	240	255	15	13	0.7	1

TABLE III
RESULTS OF GA TREATMENT ON CERTAIN MEASUREMENTS OF FOUR MAIZE TASSEL GENOTYPES AND THEIR NORMAL SIBS

Genotype	Dosage of GA in micrograms	Length of central spike (cm.)		Number of primary tassel branches		Length of tassel branching area (cm.)		Peduncle length (cm.)		Plant height (cm.)		Number of internodes		Number of ears	
		M	C	M	C	M	C	M	C	M	C	M	C	M	C
M = Vg/+ (av. of 4) C = +/+ (single plant measurements)	0	28	31	14	15	10	12	17.5	23	178	207	12.5	13	1.2	2
	50	14.5	28	18	9	10	9	13	14	155	185	14	15	2.2	2
	100	23.5	24	9	10	11	10	16	8	238	168	14	14	2	3
	150	15	25	10	10	12	13	9	21	218	234	15	15	4	0
M = Tu/+ (av. of 4) C = +/+ (single plant measurements)	0	22.5	28	21	14	13	14	17	28	176	208	11.5	13	1.2	3
	50	27	28	10	5	12	9	18	20	196	204	14	13	1.7	2
	100	28	30	13	6	13	9	14	15	203	211	13.5	14	1.2	1
	150	15	9	12	14	10	14	12	25	190	216	13	12	1.2	1
M = ra ₁ /ra ₁ (av. of 4) C = +/ra ₁ (single plant measurements)	0	11	21	64	18	31	13	23	22	155	170	11	13	2.7	3
	50	9	28	63	10	32	12	23	28	196	222	13	13	1.7	2
	100	15	30	39	14	30	10	24	11	213	256	12	15	1.7	2
	150	11	25	25	13	17	20	25	33	236	229	11.5	11	1.2	2
M = ms ₁ /ms ₁ (av. of 4) C = +/ms ₁ (single plant measurements)	0	15	22	10	14	7	9	15	19	166	202	12.5	14	1.7	2
	50	21	21	8	16	9	10	14	21	181	200	14.5	15	1.7	3
	100	13	20	11	14	8	12	15	18	199	205	15	15	1	2
	150	17	16	8	7	8	9	13	17	199	219	15	14	1.7	2

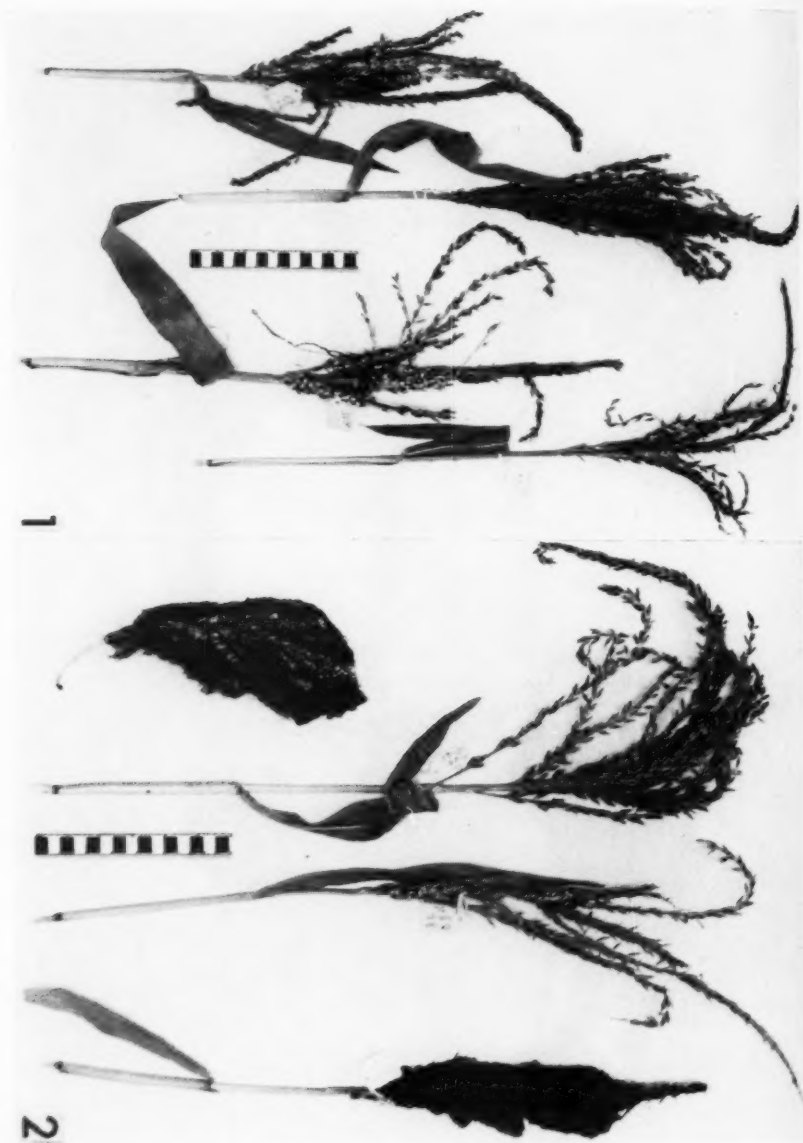
EXPLANATION OF PLATE

PLATE XII

Tassels of ts_2/ts_2 maize plants treated with, from left to right; top row, water and doses of 50 ppm GA; bottom row, doses of 100 and 150 ppm GA.



NICKERSON—GIBERELIC ACID TREATMENT II



NICKERSON—GIBERELIC ACID TREATMENT II

EXPLANATION OF PLATE

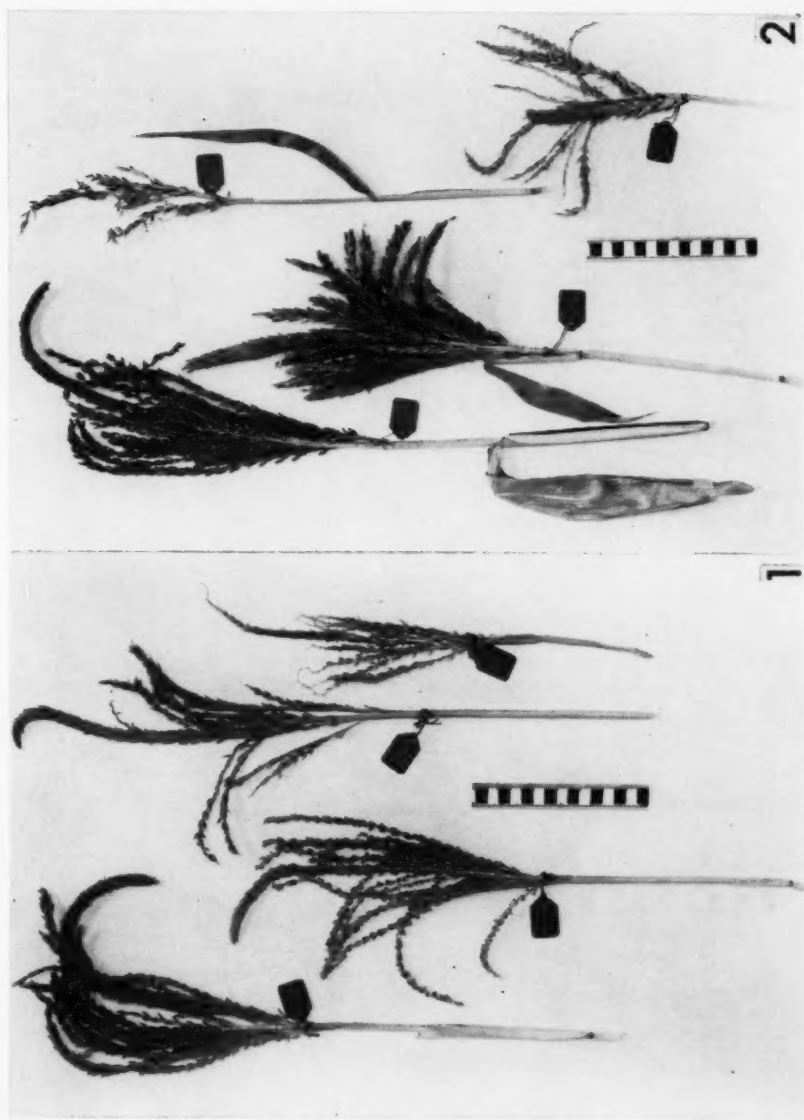
PLATE XIII

Tassels of $Ts_5/+$ (lower) and $+/+$ (1) and $Ts_6/+$ (extreme left and right) and $+/+$ (2) maize plants. Those left of ruler were treated with distilled water; those on right with doses of 150 ppm GA.

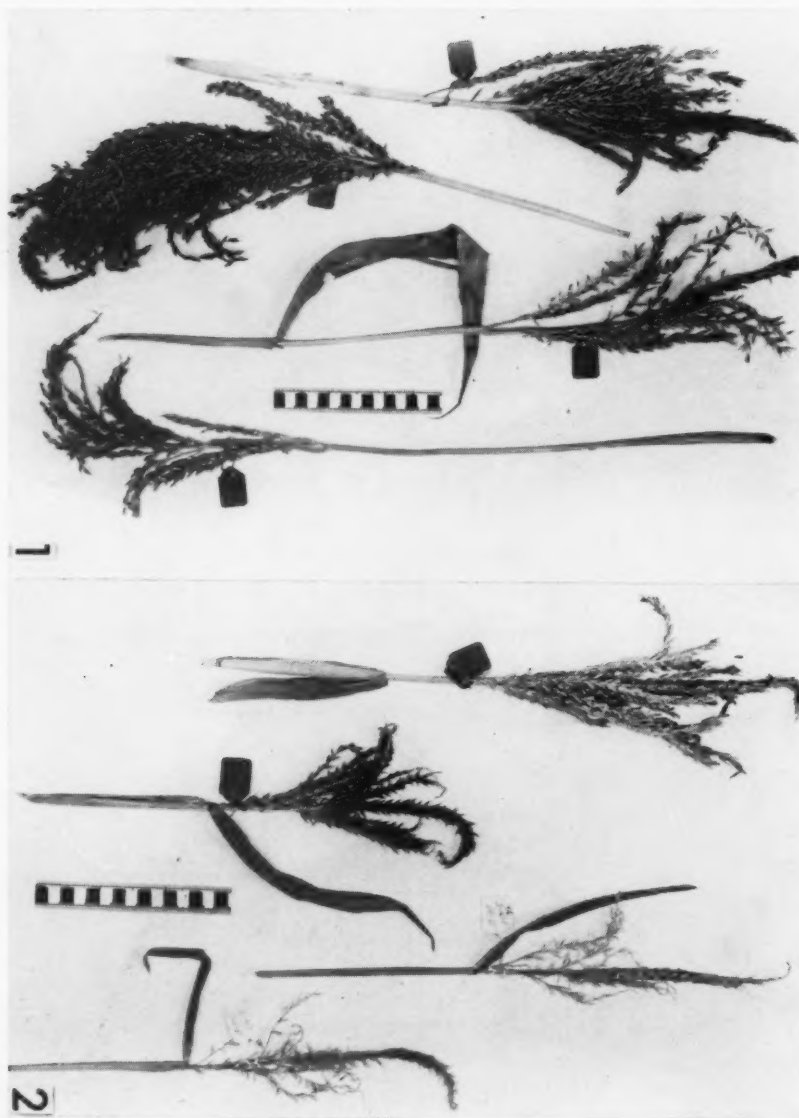
EXPLANATION OF PLATE

PLATE XIV

Tassels of Vg/+ (lower) and +/+ (1) and Tu/+ (lower) and +/+ (2) maize plants. Those left of ruler were treated with distilled water; those on right with doses of 150 ppm GA.



NICKERSON—GIBERELIC ACID TREATMENT II



NICKERSON—GIBBERELIC ACID TREATMENT II

EXPLANATION OF PLATE

PLATE XV

Tassels of ra_1/ra_1 (inverted) and $+/ra_1$ (1) and ms_1/ms_1 (lower) and $+/ms_1$ (2) maize plants. The two tassels at the left in each photograph were treated with distilled water; the two tassels at the right were treated with doses of 150 ppm GA.



